

BRITISH AVONIAN (CARBONIFEROUS)
CONODONT FAUNAS, AND THEIR VALUE
IN LOCAL AND
INTERCONTINENTAL CORRELATION



BY

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ABSTRACT

THE conodont faunas of the Lower Carboniferous of the South West Province, the Yoredales and the Midland Valley of Scotland are described. A complete series of samples was collected from the Avon Gorge section, Bristol, and also from composite sections from the North Crop of the South Wales Coalfield, the Clee Hills, Wensleydale, Dunbar, Fife, Roxburgh, Midlothian, Ayrshire and Argyll. A total of over 600 samples was collected at intervals ranging from ten feet (Avon Gorge) to six inches (Dunbar). The calcareous samples were dissolved in either 8% acetic acid or 15% formic acid, and the argillaceous samples subjected to 100 vol. hydrogen peroxide. Some 3 tons of rock was processed.

All collected sections are illustrated and charts of the conodont abundance (number of specimens per kilog.) and weight of rock dissolved, together with sample numbers, are presented. In all, the samples yielded over 25,000 identifiable specimens, referable to 167 species, belonging to 29 genera, of which 2 named genera (*Clydagnathus* and *Patrognathus*), 40 species and 13 subspecies are new. All species are described and illustrated, and range charts of their vertical distribution are presented.

The faunas are divided into a total of 14 conodont assemblage zones and correlations are made between standard sections in the various Carboniferous provinces of Great Britain. There is a strong general similarity between the succession of conodont faunas in North America, Germany and Britain, although there are also some striking local differences. These are analysed in the light of conodont phylogeny, distribution, and of possible sedimentary breaks in various sections. Correlations are made with the standard goniatite sections of Germany and with the type sections of the Mississippi Valley.

Within the South West Province the basal part of the K Zone is correlated with the Cu I goniatite zone and the upper part with Cu II α ; the uppermost K to the Upper S₂ Subzone is correlated with the Cu II Zone, and the D₁, D₂, and D₃ Subzones with the Cu III goniatite zone.

The upper part of the Calciferous Sandstone Measures of the Midland Valley of Scotland is of Cu III α age, the Lower Limestone Group is of Cu III β - γ age, and the Upper Limestone Group is of E₁-E₂ (Namurian) age.

I. PURPOSE AND SCOPE OF PRESENT STUDY

Conodonts were first described in 1856, and, although they were described in only a few papers in the subsequent seventy-five years, there is now a total of some 1,200 publications devoted to them. Doubt and controversy concerning their function and affinities remain greater now than a century ago. One recent author (Fahlbusch, 1964; see also Beckmann *et al.*, 1965) has argued that they represent algae, and another that they were internal supports in some ciliated tentacle apparatus of an unknown filter-feeding organism (Lindström, 1964), while still another (Foss, 1960) has suggested that the similarity of their carbonate fluorapatite composition to that of scales of the Ordovician chordate *Astraspis* implies an affinity between the two.

Studies of amino acid content and of ultramicroscopic structure of conodonts at present in progress may provide important new information on their affinities (Schwab, 1966 ; Armstrong & Tarlo, 1966).

In spite of the uncertainty concerning their nature and function, studies on conodont successions during the last decade have shown conodonts to be one of the most sensitive and useful fossil groups available for stratigraphic correlation. Recent work by German palaeontologists (see p. 8 for detailed references) on the conodont faunas of the type sections of the Upper Devonian and Lower Carboniferous has provided the means of making even more precise regional correlation than those recognized by goniatites upon which "standard" correlations have been established (see, for example, Ziegler 1962). Furthermore, a broadly similar zonal sequence of conodonts has been established in the Mississippi Valley.

The purpose of the present paper is to describe conodont faunas from the "Lower" Carboniferous rocks of the type section in the Avon Gorge, Bristol, from various parts of South Wales, and from Shropshire, Yorkshire and Scotland. Over 600 samples from these areas have been processed, and have yielded over 25,000 identifiable specimens. The sequence of the conodont faunas at present described provides the basis for a conodont zonation, which not only assists intra- and inter-basinal correlation in Britain, but also allows the first precise correlation with North America and Continental Europe.

II. HISTORY OF PREVIOUS RESEARCH

(a) *History of previous conodont research in Britain*

Conodonts were first described by Pander (1856) and, although they were reported shortly afterwards from several localities in Britain, comparatively little attention has been paid to them in this country.

Walliser (1958) recorded the oldest known stratigraphic occurrence in Britain, when he discovered a "paraconodont" from the Upper Cambrian Comley Limestone of Shropshire.

Ordovician conodont faunas from Britain have been described from the Arenigian of the Southern Uplands (Smith 1907 ; Lamont & Lindström 1957) ; the Llandeilian Llandeilo Limestone of Carmarthenshire (Rhodes 1953), and Castell Limestone of Pembrokeshire (Bergström 1964) ; the Upper Llandeilian and Lower Caradocian of the Southern Uplands ; the Caradocian *wilsoni* Shales of the Southern Uplands (Lindström 1957), Gelligrin, Pen-y-garnedd, Crûg and Bryn Pig Limestones of Wales (Rhodes 1953 ; Lindström 1959 ; Bergström 1964) and the Ashgillian Kiskey Limestone of Westmorland (Rhodes 1955) and Birdshill Limestone of Carmarthenshire (Bergström 1964).

A number of early workers, including Harley (1861), Moore (1864), Young (1880A) and Smith & Jones (1881), recorded conodonts from Silurian rocks in Britain.

A basal Llandovery fauna referable to the *celloni* Zone of Walliser (1964) from the Malverns was described by Brooks & Druce (1965). Llandoveryan conodonts have also been noted by Whittard (1927) from the *Pentamerus* Beds of Shropshire and by Squirrell & Tucker (1960) from the Upper Llandoveryan of the Woolhope Inlier.

Wenlockian conodonts have been collected from the Welsh Borderland by Hill (1936) and systematically described from Usk by Austin & Bassett (1967). Conodonts from the Woolhope, Wenlock, Aymestry and Whitcliffian Limestones of the Welsh Borderland were reported by Ireland (1958, 1962). Rhodes (1953) with Newall (1963) systematically described a fauna from the Aymestry Limestone of Shropshire and South Staffordshire. Squirrell & Tucker (1960) listed Upper Ludlovian conodonts from the Woolhope Inlier and Collinson & Druce (1966) systematically described a fauna from the Whitcliffe Flags of Shropshire which was referable to the *eosteinhornensis* Zone of Walliser (1964).

Dineley & Rhodes (1956) described Devonian conodonts from the Upper Givetian at Torquay, from the Lower Frasnian near Chudleigh, from the Lower Frasnian at East Ogwell and from the Lower Pilton Beds (Strunian) at Saunton, North Devon. They also described (1957) an Upper Devonian fauna from the limestones of the Bishopsteignton borehole. Matthews (1962) reported a late Eifelian fauna from a Middle Devonian limestone at Neal Point in the Tamar Valley. House (1963, table 2) and House & Selwood (1964) have summarised known Devonian conodont occurrences in South West England. The only new conodont record noted by House & Selwood was an Upper Givetian conodont fauna from the Marble Cliff Beds, identified by Rhodes. Rhodes also identified Lower Givetian conodonts from the Middle Gramscatho Limestones for Hendriks (1966). Other limestones yielding Siegenian, Emsian and Middle Devonian conodonts are also mentioned. Ziegler (Hendriks 1966) has also extracted Frasnian conodonts from limestones interstitial with the Mullion Island pillow lavas.

British Lower Carboniferous conodont studies have been few and brief. Moore (1863, 1870) listed conodonts from the Carboniferous Limestone of Yorkshire and Cumberland, Fowler (1955) mentioned conodonts obtained from a borehole in South-East County Tyrone, Eire, and Robbie (1955) reported conodonts from the Rossmore and Edenbrook beds of Lower Carboniferous age obtained from the subsurface at Edenork, County Tyrone, Ireland. Dineley & Rhodes (1956) studied eight samples from the Tournaisian of South West England. Small faunas from the Shirehampton Beds, the Lower Limestone Shale, the Black Rock Limestone, the Fish Bed and Horizon γ , collected in the Avon Gorge, Bristol, were described, as also were faunas from the ? Black Rock Limestones of Windsor Hill, Somerset and Waterlip Quarry, Somerset. Matthews (1961, 1966) has identified *anchoralis* faunas collected at Viverdon Down near Callington, and from the St. Mellion area of South West England. Varker (1967) has described conodonts referable to the genus *Apatognathus* from the Yoredales of Northern England.

Young (1880, 1880A) mentioned the occurrence of Scottish Carboniferous Limestone conodonts, in addition to those of the Silurian and Devonian of England. Smith (1900) reported conodonts from the Carboniferous limestones of Western Scotland and figured those described by Hinde (1879, 1900). These were subsequently refigured and redescribed by Clarke (1960) who also described faunas from the Scottish Carboniferous Limestone Series. Craig (1952, 1954) reported conodonts from the Top Hosie Shale, of Lower Carboniferous age, near Kilsyth, Scotland.

Namurian conodonts were found in a borehole in a Yoredale type of deposit in the Cleveland Hills by Fowler (1944). Dunham & Stubblefield (1945) noted the occurrence of a platform conodont in the Colsterdale Marine Beds of the Millstone Grit of Yorkshire. Conodonts have also been noted in the Millstone Grit of the Midlands by Stevenson & Mitchell (1955). The only published systematic description of British Namurian conodonts is that by Higgins (1961) who described a fauna from the Namurian of North Staffordshire. Collinson & Druce (*in press*) have described a conodont fauna from the lower boundary of the Namurian in County Clare, Eire.

There have been no detailed systematic descriptions of British Pennsylvanian conodonts, but many workers have noted the presence of conodonts in the British Coal Measures. In Scotland, Currie, Duncan & Muir-Wood (1937) described conodonts from Skipsey's Marine Band, and the Upper Coal Measures in Central and West Scotland. Manson (1957) listed conodonts from a marine band in the *Anthraconaia modiolaris* Zone of Scotland. Smith (1907A) recorded conodonts from the Upper Coal Measures (above the Craigmere Ironstone).

Stevenson & Mitchell (1955), Stubblefield & Calver (1955), Mitchell (1954) and Eden (1954) reported conodonts from the Midland Coalfields, as also have Mitchell & Stubblefield (1941) from the Leicestershire and South Derbyshire Coalfield, Mitchell, Stubblefield & Crookall (1942, 1945) from the Warwickshire and northern part of the South Staffordshire Coalfields, Edwards & Stubblefield (1948) from the Derbyshire and Nottinghamshire Coalfields, and Edwards (1954) from the Clown Marine Band in Derbyshire and Nottinghamshire. Earp & Magraw (1955) listed conodonts from the Tonge's Marine Band in the Lower Coal Measures of Lancashire, and Magraw (1957) recorded conodonts from various marine bands in Lancashire, Derbyshire and Yorkshire. Ramsbottom (1952) and Woodland, Archer, Evans & Calver (1957) noted the presence of conodonts in the South Wales Coal Measures.

There has been no reference to the occurrence of post-Pennsylvanian conodonts in the British Isles.

(b) *Carboniferous conodont zonation and correlation*

Although the Upper Devonian and Lower Carboniferous rocks of West Germany, the latter of which provide the standard for Carboniferous correlation, are traditionally correlated on the basis of their cephalopod faunas, recent studies by German palaeontologists on the conodont faunas have shown that the latter offer a new degree of precision in problems of regional correlation. The most notable contributions in this field are those of Bischoff (1955, 1956, 1957), Bischoff & Ziegler (1956, 1957), Bartenstein & Bischoff (1962), Böger (1962), Kronberg, Pilger, Scherp & Ziegler (1960), Meischner (1962), Sannemann (1955, 1955A), Voges (1959, 1960), Walliser (1958, 1960) and Ziegler (1958, 1959, 1962, 1962A, 1962B). These workers described conodonts, which were associated with the classic Devonian and Lower Carboniferous cephalopod zones in West Germany, and a detailed Devonian and Lower Carboniferous conodont faunal succession has thus been established.

This conodont succession has been applied to rocks of Upper Devonian and Carboniferous age in other parts of Western Europe, notably by Dvorak & Freyer (1961), Helms (1959, 1961), and Müller (1959) in East Germany ; Flugel & Ziegler (1957) in Austria ; Lys & Serre (1958), Higgins (1962), Higgins, Wagner-Gentis & Wagner (1964) in Spain ; Lys & Serre (1957), Lys, Serre & Deroo (1957), Lys, Serre, Mauvier & Grekoff (1961) in France and the Sahara ; Boogaard (1963) in Portugal ; and by Serre & Lys (1960) and Conil, Lys & Mauvier (1964) in Belgium.

Germany

The zonation of the Lower Carboniferous in Germany is based chiefly on the work of Bischoff (1957) and Voges (1959).

Bischoff (1957) studied the conodont faunas of the *Wocklumeria*, *Gattendorfia*, *Pericyclus* and *Goniatites* Stages of the Rhenohertzynicum. He subdivided the *Pericyclus* Stage into two conodont subzones—the *Siphonodella* Subzone (Cull α - β) and the *anchoralis* Subzone (Cull γ). He also described the conodont faunas of the three goniatite zones of the *Goniatites* Stage.

Voges (1959) described conodonts from the Lower Carboniferous *Gattendorfia* and *Pericyclus* Stages. He recognized three zones within the *Gattendorfia* Stage : the *Gnathodus kockeli*-*Pseudopolygnathus dentilineatus* Zone ; the *Siphonodella*-*Pseudopolygnathus triangulus inaequalis* Zone and the *Siphonodella*-*Pseudopolygnathus triangulus triangulus* Zone. Three zones were recognized by Voges within the *Pericyclus* Stage ; the *Siphonodella crenulata* Zone (Cu II α), which was subdivided into a lower and an upper subzone, the *Scaliognathus anchoralis* Zone (Cu II $\beta\gamma$), and a *Scaliognathus anchoralis*-*Gnathodus bilineatus* "interregnum" (Cu II δ). Voges thus gave a more detailed and refined zonation than Bischoff (1957) for the *Gattendorfia* and *Pericyclus* Stages, and also differed from Bischoff by extending the *Scaliognathus anchoralis* Zone into Cu II β (Bischoff confined the *anchoralis* Zone to Cu II γ).

The German workers were thus the first to attempt a conodont zonation of the Lower Carboniferous. Whilst not detracting in the least from the excellent work of Bischoff and of Voges it is true to say that there are a number of deficiencies and gaps in our knowledge of German conodont faunas. The reasons for these gaps are twofold. Firstly the nature of the outcrops is such that it is impossible to collect from continuous exposures. The different samples collected by both Voges and Bischoff are from widely separated areas. Secondly, the sediments are such that in any one locality not all horizons yield conodonts (e.g. Hangenberg Schiefer, and the cherts immediately beneath the "Erdbach Kalk"). There has also been a marked tendency for German conodont workers to give total stratigraphic ranges of species, rather than the exact distribution and abundance of individual species, although more recently, for example Kronberg, Pilger, Scherp & Ziegler (1960) and Ziegler (1963), these have been given. It is becoming increasingly apparent from conodont studies in other parts of the world that numbers of stratigraphic breaks exist in the German succession, even where these have not hitherto been suspected.

The Franco-Belgian Province

Studies of the Franco-Belgian Lower Carboniferous conodont faunas are comparatively recent. Serre & Lys (1960) described the distribution of Tournaisian and Viséan conodonts in the Avesnois, Boulonnais and Hainault regions of Northern France and Belgium, and Conil, Lys & Mauvier (1964) recorded the ranges of conodont species in the type formations of the Dinantian in the Franco-Belgian Province. More recently Bouckaert & Ziegler (1965) have published an account of the conodont faunas of the Famennian Stage in Belgium.

Conodont studies in the Franco-Belgian Province are important because these sections have yielded the type specimens of many Lower Carboniferous cephalopods. Unfortunately, however, neither Serre & Lys nor Conil, Lys & Mauvier have systematically described or illustrated their specimens, and they have given no exact distribution or abundance data for individual species. Thus the work at present is of limited value. Few correlations can be made, although one which can be made with a fair degree of certainty is based on the distribution of *Scaliognathus anchoralis*. This species is restricted to Tn_{3b} in the Franco-Belgian Province and to the Cu II β γ horizon in Germany. This is important, because hitherto it has been considered likely that the Tournaisian-Viséan boundary in Germany should be drawn at the base of Cu II β γ , based on the distribution of *Pericyclus princeps*. This is the zonal fossil for Cu II α in Germany and was first found and described from the Tn 3c of Belgium. If the conodont correlations based on *anchoralis* are accepted, they are at variance with the "well established" goniatite evidence, although the literature does not contain a single reference to *Pericyclus princeps* having ever been found in Germany. It is therefore a very dubious "zonal fossil".

The need for systematic descriptions and illustrations of the Franco-Belgian conodonts is thus urgent for it may provide the key for unravelling the German succession and for filling the gaps which are present in Germany.

The United States

Lower Carboniferous conodont research in North America began in the mid nineteen-thirties. Huddle (1934) described the conodont fauna of the New Albany Shale in Indiana and Branson & Mehl, working in Missouri, described the conodont faunas of the Bushberg Sandstone (1934A), of the "Lower Mississippian Formations" (1938A), of the Caney Formation (1940) and of the Keokuk Formation in Iowa and Missouri (1941A). E. R. Branson (1934) also described conodonts from the Hannibal Formation in Missouri.

Cooper (1939) described conodonts from the Bushberg Hannibal strata in Oklahoma and later, with Sloss (1943), described a fauna from a Lower Mississippian black shale in Montana and Alberta.

Mehl & Thomas (1947) described the conodont fauna of the Fern Glen Formation in Missouri, and Thomas (1949) described the faunas of Lower Mississippian age from the English River and Prospect Hill Siltstones of South East Iowa.

Hass described Lower Carboniferous conodonts from the Arkansas Novaculite of

Arkansas (1956A), the Maury Shale of Tennessee (1956), the Barnett Formation (1953) and the Chappel Limestone of Texas (1959).

Scott & Collinson (1961) described a fauna from the Louisiana Limestone and from the McCraney Limestone.

Youngquist & Patterson (1949) described conodonts from the Prospect Hill Sandstone of Iowa. The fauna of the Lower Mississippian Wassonville Dolomite of Iowa was described by Youngquist & Downs (1951). Youngquist, Miller & Downs (1950) described Burlington conodonts from Iowa.

Rexroad (1957) described Chester conodonts from Illinois and later (1958) from the Glen Dean Formation. Rexroad & Clarke (1960) described Glen Dean conodonts from Kentucky, Virginia and West Virginia. Golconda Group conodonts were described by Rexroad & Jarrell (1961). Those of the Kinkaid Formation in Illinois were described by Rexroad & Burton (1961) and those of the Paoli and equivalent formations in Illinois by Rexroad & Liebe (1962).

From the work of these and other workers, it became clear that conodonts were abundant in Mississippian rocks and were useful for correlation of strata. As a result, the Illinois State Geological Survey, in co-operation with the University of Texas, the State University of Iowa, Texas Technological College, the University of Houston, and the Indiana Geological Survey, conducted a programme of research in the Mississippi Valley. In 1962 Collinson, Scott & Rexroad published a paper in which they described 17 conodont biostratigraphic zones, which were present in the Mississippian rocks of the Mississippi Valley. The limits and characteristic species of each zone were described and they also attempted to correlate these zones with the conodont zones present in Germany.

Subsequent workers have systematically described the faunas of the biostratigraphic zones established in 1962. Thus Rexroad & Collinson (1963) not only described the conodonts of the St. Louis Formation, but also indicated, described and illustrated the species characteristic of the *Taphrognathus varians*-*Apatognathus* Assemblage Zone and of the *Apatognathus* ? *geminus*-*Cavusgnathus* Assemblage Zone.

In the same way Rexroad & Scott (1964) when describing the conodont faunas of the Rockford Limestone and the lower part of the New Providence Shale of Indiana described and illustrated the conodont fauna characteristic of the *Siphonodella isosticha*-*S. cooperi*, *Gnathodus semiglaber*-*Pseudopolygnathus multistriatus*, *Bactrognathus*-*Polygnathus communis* and *Bactrognathus*-*Taphrognathus* Assemblage Zones. They also showed in tables the numerical distribution and stratigraphic ranges of specimens.

Rexroad & Collinson (1965) provided the same data for the *Taphrognathus varians*-*Apatognathus* Assemblage Zone, when describing the conodonts of the Keokuk, Warsaw and Salem Formations of Illinois.

Rexroad & Furnish (1964) referred their fauna from the Pella Formation of South-Central Iowa to the *Gnathodus bilineatus*-*Cavusgnathus charactus* Assemblage Zone of the Mississippi Valley, and to the St. Genevieve Limestone in particular.

Rexroad & Nicoll (1965) described the faunas of the Menard Formation, which they referred to the *Kladognathus*-*Cavusgnathus naviculus* Zone, drawing the lower

limit of that zone at the base of the Menard. Klapper (1966) described Upper Devonian and Lower Mississippian faunas from Montana, Wyoming and South Dakota, and identified the local equivalents of the German Cu I and Cu II α faunas.

These studies have provided a most useful basis for the correlation of our Avonian faunas with those of the Mississippi Valley.

Australia

Recent studies by Glenister & Crespin (1959), Glenister (1960), Jones & Druce (1966) and Glenister & Klapper (1966) have shown the similarity of European-North American Devonian and Lower Carboniferous conodont faunas to those of comparable age in Australia.

III. STRATIGRAPHY

(a) *Introduction to the stratigraphy of the Carboniferous of Britain*

Rocks of Lower Carboniferous age form one of the most extensive outcrop belts in the geology of Britain but, in spite of their extensive outcrop, generally good exposure, and the wealth of study devoted to them, precise correlation is often difficult between basins, and sometimes also within them. The distribution and character of Lower Carboniferous rocks is so well known that it needs only the merest introduction in a study such as this, as it has recently been reviewed by George (1958).

Lower Carboniferous rocks were deposited on an archipelago-like basement (Fig. 1) dominated by a landmass to the north-west, by a caledonoid-trending massif which extended from north-eastern Ireland into the Southern Uplands, by a stable block in north-eastern England, and a great, east-west landmass, stretching from Leinster through Central Wales into the Midlands of England. To the south of this landmass, the south-western Province of the Carboniferous represented a basin of more or less continuous deposition, which extended westwards into Ireland and was bounded by a landmass in south-western Cornwall. It was marked by the deposition of two distinctive facies groups. In the south, the Culm facies of Devon and Cornwall and southern Ireland included dark argillaceous and sometimes calcareous shales and mudstones, containing a few thin, impure, dark limestones and cherts, as well as subordinate sandstones and grits. To the north of this facies, in Somerset, Gloucestershire and South Wales, there was deposited the "limestone facies," consisting mainly of grey or light-blue bioclastic limestones, with subordinate dolomites, oolites and argillaceous limestones. These rocks contain a rich fauna of brachiopods and corals, as well as crinoids, ostracods, foraminifera and algae. In some parts of the section there is developed a "lagoon" facies, characterized by drab grey, calcite-mudstones, with subordinate calcareous shales and oolitic rocks. Calcareous algae, ostracods, gastropods and pelecypods are the main fossils of this group, which is present in the *Modiola* phase of south-western England. Both the Culm facies and the bioclastic limestone facies extend westwards into southern Ireland.

Northern England was separated from Southern England for at least part of Carboniferous times, by the combined St. George's Land-Midland Barrier. In the

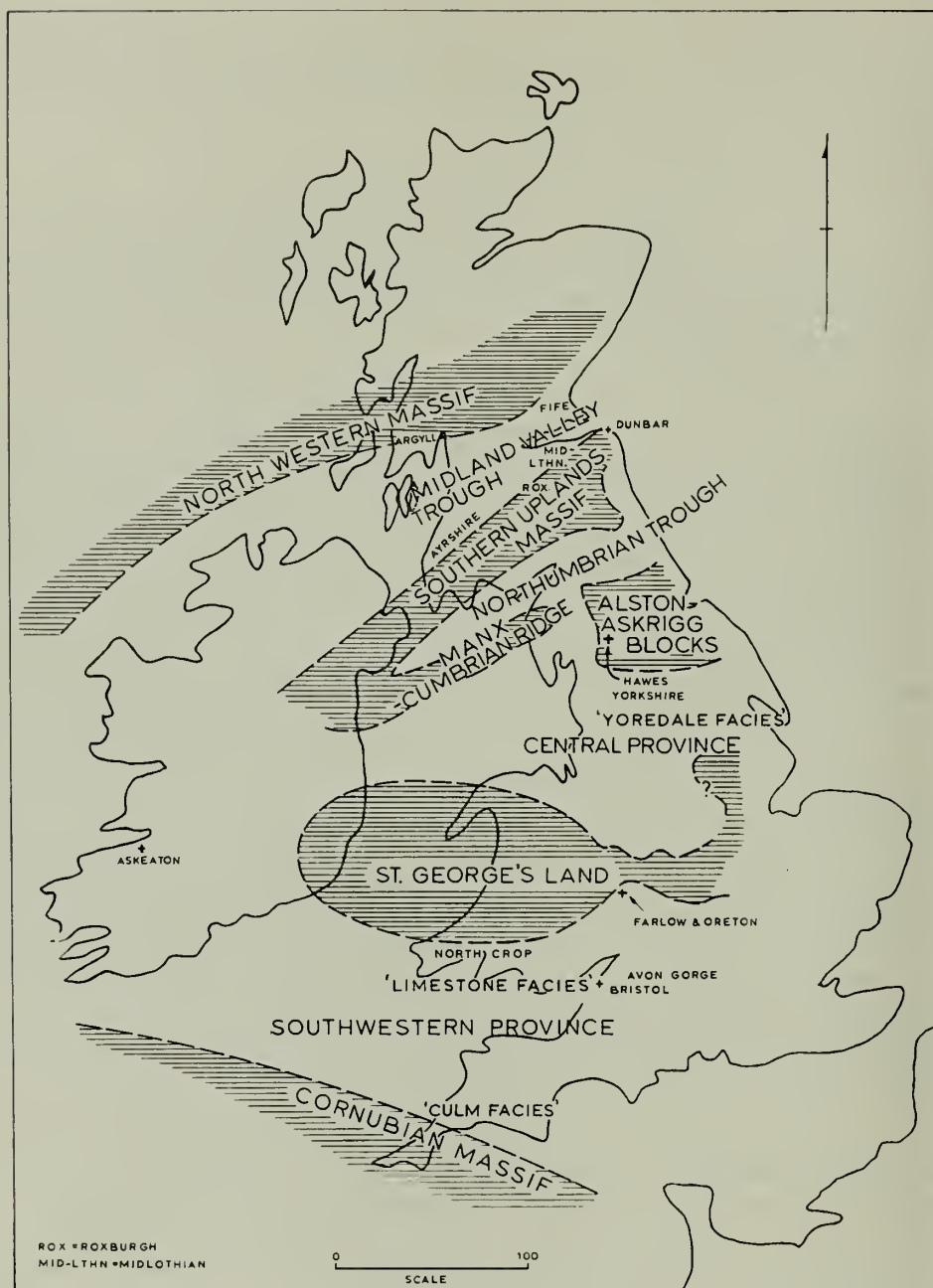


FIG. 1. Generalized palaeogeographic map of Britain during Early Carboniferous times, showing main depositional régimes, and localities described in the text. Based partly on George (1958) and Wills (1952).

Central Province, lying to the north of this barrier, rocks of Yoredale facies were deposited. These include cyclothemic limestones, non-marine sandstones, shale, and coal sequences, with a fauna of corals, brachiopods, bivalves, occasional goniatites and non-marine plants. Bioclastic limestones and spectacular reefs also developed in various places in this region, such as the reef knolls of Derbyshire and the Craven Lowlands, and the larger sheet-like apron reefs of Southern Ireland.

In the Northumbrian trough, lying to the north of the Central Province, as well as in the trough of the Midland Valley of Scotland, which was separated from it, a distinctive facies of the Cementstone type was developed, consisting of alternating thin argillaceous limestones, sandstones and grey-black shales. Fossils are rare and include fish, ostracods, inarticulate brachiopods and spirorbid worms. These rocks are overlain by sandstones, coal-bearing strata and limestones, the total Northumbrian section including some 7,000 ft. of strata. In the Midland Valley of Scotland, a broadly similar variety of rock types is found, although there is no detailed equivalence in age; clastic deposits predominate there, and include the Oil Shales and the Calciferous Sandstones. There are also thick lavas in places.

In north-western Ireland great thicknesses of deltaic strata were deposited, which pass southwards into limestone-shale and bioclastic limestones (George 1955).

Rocks of Lower Carboniferous age present formidable problems of correlation and these arise largely from the rapid and almost continuous lithological and faunal changes which they display. The general problems of correlation have been reviewed by Rayner (1953) and by George (1952 and 1958). The first successful attempt to provide a palaeontological subdivision of the rocks of the South-West Province was that of Vaughan (1905) who proposed the now widely-applied coral-brachiopod system for the limestones of south western England. This was based upon exhaustive and meticulous collecting of faunas, especially from the Avon Gorge. Vaughan established his zonal scheme on the first appearance of particular genera and species, although the zones as interpreted today are partly assemblage zones, based on the occurrence of a number of species. To a varying extent the demarcation of Vaughan's zones was influenced by the marked lithological changes which occur in the Avonian strata of south-western England (see p. 17).

It was early recognized that Vaughan's zonal scheme was inapplicable to the different facies of northern England and in that area the work of Bisat (1924) on goniatites provided the basis for much of the present classification.

Present views on the validity of these various zonal schemes are sharply divided. There is general agreement that, in the sense in which they were originally established by Vaughan, the coral-brachiopod zones can no longer be applied in detail, but some workers, especially Kellaway & Welch (1955), reject the whole zonal scheme which they represent. The detailed problems of correlation are discussed on p. 52.

(b) *The Avonian Succession*

The Avon Gorge, Bristol, has long been regarded as the type area for the British "Lower" Carboniferous. The base of the Lower Limestone Shale was selected by Buckland & Conybeare (1824) and by De la Beche (1846) as the base of the Lower

VAUGHAN (1915)		VAUGHAN (1905)					VAUGHAN (1906)	DIXON AND VAUGHAN (1911)	REYNOLDS AND VAUGHAN (1911)	VAUGHAN (1915)	DIXEY AND SIBLEY (1918)
Z A F S I V	V _{2c}	DIBUNOPHYLLUM ZONE D					D ₂	D ₂	D ₂	D ₂	D ₂
		D ₁					D ₁	D ₁	D ₁	D ₁	D ₁
V	V _{2cx}	SEMINULA ZONE S					S ₂	S ₂	S ₂	S ₂	S ₂
		S ₁					S ₁	S ₁	S ₁	S ₁	S ₁
	V _{2a}										
TOURNAISIAN (= end VAUGHAN)	T ₂	UPPER CANINIA ZONE					S ₁	S ₁	S ₁	S ₁	UPPER CANINIA ZONE C ₂ S ₁
		LOWER CANINIA ZONE					C ₂	C ₂	C ₂	C ₂	LOWER CANINIA ZONE C ₁
DEVONIAN	F _{a2}	SYRINGOTHYRIS ZONE C					C	C ₁	C ₁	C ₁	Z
		ZAPHRENTIS ZONE Z					Lom Dol				K
		CLEISTOPORA ZONE K					Y	Y	Y	Y	K
											--- VISEAN - TOURNAISIAN BOUNDARY

FIG. 2. The subdivision of the Avonian, showing the original zonation of Vaughan and later refinements.

Carboniferous. Although Vaughan (1905) established a series of coral-brachiopod zones for the succession, these were later found to be of only local value in correlation (see George 1952, 1958 for a critical review), so that other type sections have been recognized for other areas of Britain (e.g. Walker 1964). The accepted international type section for the Lower Carboniferous is that in West Germany.

The rocks of the Avon Gorge comprise some 3,000 ft. of strata, consisting predominantly of carbonates, but with subordinate shales and sandstones. Vaughan (1905) subdivided these into five faunal zones, four of which were divided into two subzones (Fig. 2). Vaughan pointed out that the Dinantian was approximately, but not exactly, equivalent to his Avonian, which he subdivided into the underlying Clevedonian (C, Z, K) and the Kidwellian (D and S Zones), rather than using the equivalent Tournaisian and Viséan. Vaughan modified his classification in later publications (1906, 1915 : Dixon & Vaughan 1911, Reynolds & Vaughan 1911). The modifications involved the inclusion of the *Modiola* phase as the basal subzone of K (Km), the varying position of horizon γ (included in Z in 1905 ; in C in 1911 ; included as the major part of C in Burrington Combe in 1911), and the development of the *Caninia* Zone (1906, 1911). Other authors also proposed subsequent amendments, Dixey & Sibly (1918) subdividing the C Zone in South Wales, and Hudson & Dunnington (1945) placing the *Caninia* Oolite in the Upper C Zone.

The present standard coral-brachiopod zonation of the Avonian (modified after George 1958) is as follows :

<i>Symbols</i>			
6	DIBUNOPHYLLUM ZONE	D	Vaughan (1905) Subzones D ₂ and D ₁ .
5	SEMINULA ZONE	S ₂	Vaughan (1905) "Main <i>Seminula</i> Zone" of Dixey & Sibly (1918).
4	UPPER CANINIA ZONE	C ₂ S ₁	Dixey & Sibly (1918). This includes part of Vaughan's (1905) <i>Syringothyris</i> Zone and the overlying Lower <i>Seminula</i> Zone (S ₁). The lower limit of this zone is placed at the top of the <i>Caninia</i> Oolite.
3	LOWER CANINIA ZONE	C ₁	Dixey & Sibly (1918), with horizon γ at the base.
2	ZAPHRENTIS ZONE	Z	Vaughan (1905) Subzones Z ₂ and Z ₁ .
1	CLEISTOPORA ZONE	K	M and K Zones of Vaughan (1905) and the K Zone of Sibly (1906).

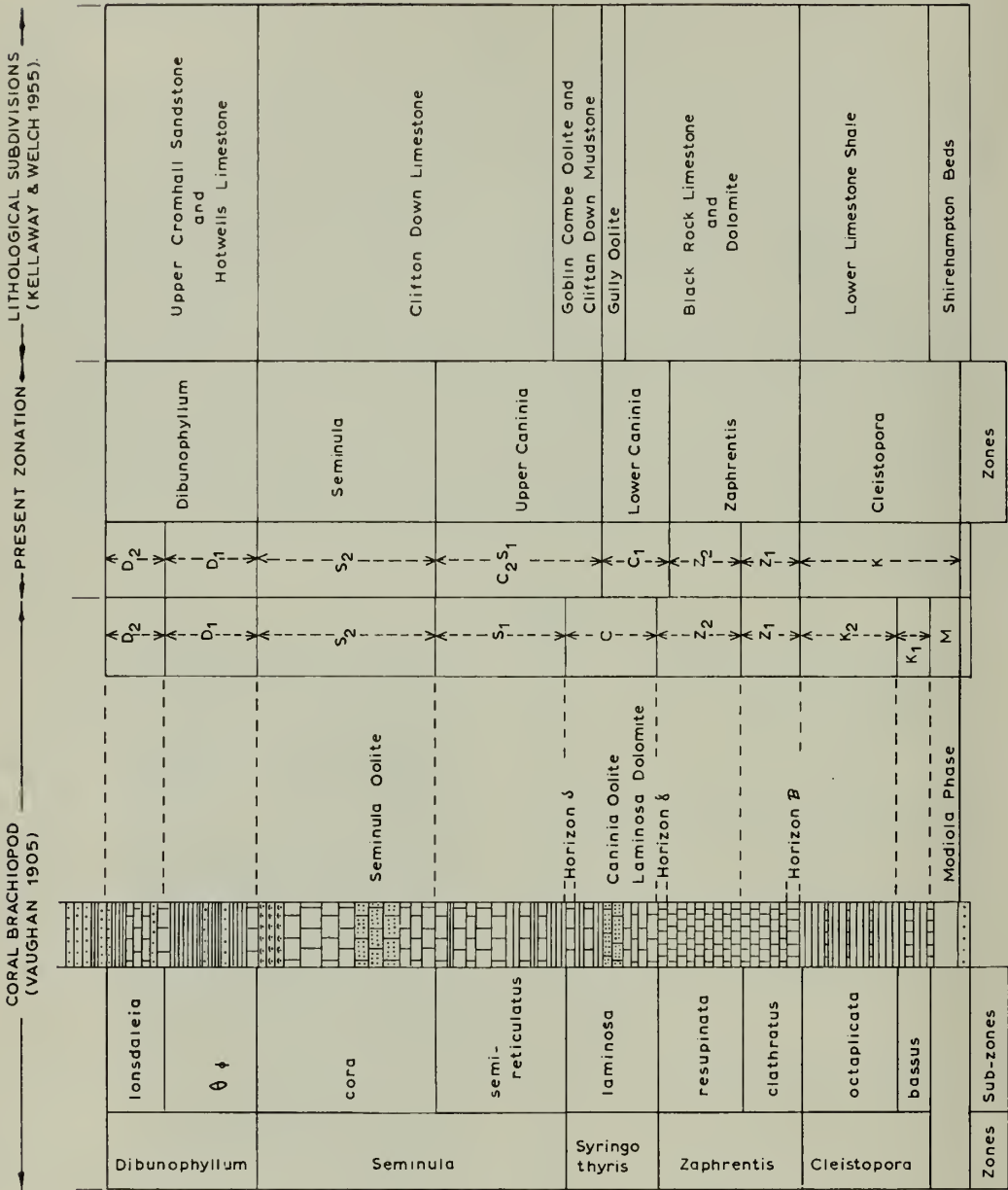


FIG. 3. Chart to show the original zonation of the Avonian by Vaughan, the present modified zonation, and the lithological subdivisions proposed by Kellaway & Welch (1955).

In this succession, Zones 1-3 are generally regarded as Tournaisian, and Zones 4-6 as Viséan.

Vaughan's general zonal scheme has been the subject of much subsequent criticism, partly because of the extent to which the distribution of corals and brachiopods is influenced by environment, and partly also because of the lack of precision in defining boundaries. The K Zone, for example, was coincident with the lithological limits of the Lower Limestone Shale, its only fossil of any possible diagnostic value being *Avonia bassus* (George 1952). The faunas of other zones were no less reflections of the facies changes represented by successive strata, the zaphrentid corals being but one example. In other areas, zonal fossil genera were found beyond the limits of these zones.

It was for these reasons that Kellaway & Welch (1955) suggested the replacement of Vaughan's zones by a succession of lithological units (Fig. 3). The object of these was to assist in regional mapping, but such lithological units are of less value in correlation than Vaughan's imperfect faunal zones. Even Kellaway & Welch, whose divisions generally correspond with the limits of Vaughan's faunal zones, found lateral transition within this area, the Shirehampton Beds of Bristol passing southwards into the base of the Lower Limestone Shale, and northwards and westwards into the top of the Portishead Beds.

Vaughan's faunal assemblage zones, defined by twin zonal indices, but strengthened and supplemented by other index fossils, still seem to us to represent the most satisfactory method of correlation in the field, although we believe that the conodont zonation presented in the present paper provides a far more precise alternative for those strata in which conodonts are present.

(c) *Previous research on the correlation of the Avonian with the Carboniferous of Europe*

The correlation of the British Avonian with the continental succession has presented acute problems. Vaughan (1915) attempted to use the coral-brachiopod faunas to correlate with the Belgian succession. He correlated the Lower Tournaisian (T_1) with his Z Zone and the Upper Tournaisian (T_2) with his C Zone (including the γ horizon), making detailed correlations within the various units. He suggested that the faunal overlap (the *Sublaevis* Beds and the Marbre Noir Series) between the Viséan and Tournaisian in the Dinantian succession was equivalent to the Upper C_2 and S_1 Zones, and the Viséan succession above V_{1a} up to and including V_{2cx} to the S Zone. He correlated the Lower V_{2c} Beds with the D_1 , and the Upper V_{2c} with the D_2 of the Avon Gorge. Vaughan correlated the Hastière Limestone and Shale, the "*Octoplicata*" Shale, and the base of the Landelies Limestone with his β horizon, but Paul (1937), on the basis of brachiopod faunas, suggested the equivalence of the upper part of K_1 and of K_2 in the Avon Gorge with the Hastière Limestone (Tn_{1b}). He regarded the Hastière Limestone and the *Peracuta* Shale (Tn_{2a}) as equivalent to the *Gattendorfia* Hangenberg Limestone of Germany, but Goldring (1958) suggested from their trilobite faunas that both these formations may be equivalent to the Lower Limestone Shale (K_1 and K_2), and he correlated the base of the Black Rock Limestone (Z_1) with the base of the Landelies Limestone (Tn_{2b}).

The outstanding difficulty of detailed correlation of the Avonian with the Carboniferous type sections of the Rheinisches Schiefergebirge has been the absence of goniatites in the type Avonian section. A prolecanitid (*Protocanites*) (identified by Professor Frank Hodson) from shales near Abergavenny may have been collected from the lithologically similar shales at the top of the Z Zone or from the K Zone. The exact locality is not specified on the specimen, which is in the Geological Survey Collections (No. G.S.M. 82817) (see also George 1952 : 35). George & Howell (1939) have described *Prolecanites discoides*, *Muensteroceras inconstans*, and *Pericyclus kochi* from the Upper *Caninia* Oolite of Three Cliffs Bay, Gower, and these suggest an uppermost Tournaisian age for these beds, while the presence of *Muensteroceras euryomphalus* and *Merocanites* cf. *compressus* in the overlying Upper *Caninia* Beds suggest a low Viséan age (George & Ponsford, 1935). The traditional Lower–Upper Avonian boundary (Dixon & Vaughan, 1912) of the Lower *Caninia* Zone (C₁) and Upper *Caninia* Zone (C₂S₁) is thus approximately equivalent to that of the Tournaisian and Viséan (see George 1952, 1955). Smith (1942 : 338) recorded a goniatite indicative of a P₂ age from the Avonian Tanhouse Beds (D₃) of the Yate district in Gloucestershire.

Currie (1954) provided a monographic study of Scottish Carboniferous goniatites which allowed her to make correlations with the stages established by Bisat. She was able to assign the Upper Limestone Group to the E₂ (Arnsbergian) Stage, the Limestone Coal Group to the E₁ (Pendleian), both the latter being of Lower Namurian age, the Lower Limestone Group to the P₂ and the Upper and higher part of the Lower Oil Shale Group of the Calciferous Sandstone 'Series' to the P₁ and B Stages (Bollandian and Cracoean) of the Middle and Upper Viséan. Bisat's B₂, P₁ and P₂ goniatite zones are equivalent to Vaughan's *Dibunophyllum* Zone, and his B₁ Zone to the main *Seminula* Zone. Prentice & Thomas (1965 : 43, Fig. 2) have given a distribution table of British prolecanitids in which they show a correlation of Vaughan's D–C Zones in North Devon with the European goniatite zones, although they provide no detailed discussion of the broader aspects of correlation.

In spite of these various studies, Lower Carboniferous correlations between Britain and continental Europe remain tenuous, the uncertainties arising chiefly from the absence of the more stratigraphically useful faunal groups common to the two areas. We believe that the closely comparable conodont faunas here described allow a far more refined correlation than any yet achieved.

(d) *The stratigraphy of areas from which conodonts are described*

(i). The Avon Gorge, Bristol.

The Avon Gorge, Bristol, is the type area for the British Avonian. A series of steep, river-side cliffs, provide almost continuous exposures of rocks from the uppermost Old Red Sandstones at the base, to the highest beds of the D Zone of the Carboniferous at the top.

The lowest beds of the Avonian section are thinly-bedded, grey, brown, green and red, marly claystones, thin grits, sandstones and fissile, slightly calcareous shales. There are few calcareous deposits, the first limestone occurring 12 ft. above the base

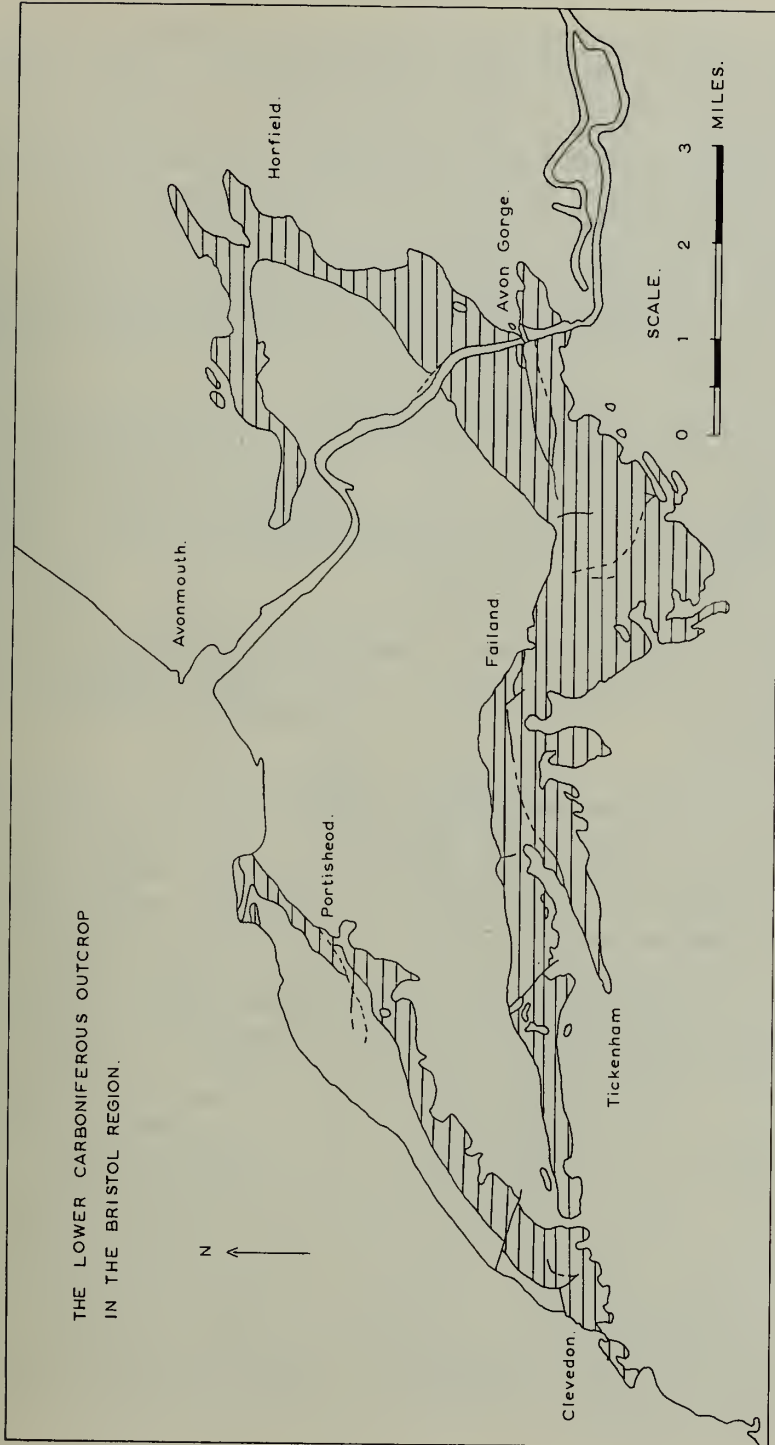


FIG. 4. The Lower Carboniferous outcrop in the Bristol area. Carboniferous Limestone is shaded with horizontal lines. Based on maps of the Geological Survey.

of the section. In the lower portion of the section fossils are rare, ostracods, gastropods and algae being the most common; brachiopods and bivalves are generally rare. Ascending the sequence, fine grained compact limestones become more prominent, their upper bedding surfaces being covered with brachiopods and crinoids. The upper part of the Lower *Cleistopora* Beds is an alternating sequence of claystones and thin limestones, which has a banded appearance. Occasional more massive limestone bands, about one foot thick, are also interbedded.

The highest beds of the shallow-water phase consist of seven distinct beds, separated by thin shale partings. The lower six beds range from 11 inches to $2\frac{1}{2}$ feet in thickness and are crinoidal limestones, which have been stained by haematite. The uppermost bed (the Bryozoa Bed) is a massive, limestone bed, eight feet thick, crowded with crinoids, bryozoa and small gastropods.

The Upper *Cleistopora* Zone consists at the base of sandy fossiliferous limestones with interbedded calcareous shales. Near the base is a "gritty" six inch bed of crinoidal limestone, the Palate Bed, which contains bryozoa, palatal teeth and coprolites. Thinly bedded limestones, and alternating shales follow. The uppermost beds of the K Zone consist of blue-grey calcarenite beds, up to one and a half feet thick, and alternating brown silty shales.

Horizon β consists of thinly bedded, coarse crinoidal limestone, with thin shale layers developed between the more massive limestone bands. The beds of the main Z Zone are blue-grey fossiliferous massive limestones, with some alternating, thinly bedded limestones and a few shale partings. The limestones approach a "petit granit" in character.

The *Laminosa* Dolomites were probably originally identical to the Z Beds in lithology, but subsequent dolomitisation has resulted in these beds weathering to a brownish colour, which contrasts strongly with the blue-grey limestones of the *Zaphrentis* Zone beneath and with the white oolites of the *Caninia* Zone above.

The *Caninia* Oolite is a pinkish-grey, white-weathering, current-bedded, fine grained oolite with uniformly rounded grains. It is succeeded by a series of current-bedded, marly limestones, dolomitic limestones, occasional oolitic bands and blue, grey, yellow, green or red shales—the *Caninia* Dolomites and Shales. The uppermost beds of this group are more massive than the lower and less shale is developed in them.

Shales and thick bands of dolomite with occasional oolites form the lowest beds of the *Seminula* Zone. They are essentially similar in lithology to the underlying *Caninia* Dolomites. They are followed by massive blue-grey limestones, which are frequently dolomitised, and by thin shales, which are succeeded in turn by calcite mudstones, which weather white. The shales become less conspicuous higher in the section, where grey *Lithostrotion*-bearing limestones predominate. The upper beds of the *Seminula* Zone, the S_2 Subzone, consist of oolites and pisolites at the base and the Concretionary Beds at the top. The latter are fine-grained, argillaceous limestones, the upper surfaces of which are undulating. They are underlain by black shales, which ramify into the overlying limestone bands. The Concretionary Beds, which sometimes contain algae and ostracods, are interbedded with chinastones and occasional oolitic limestones.

Massive grey foraminifera-bearing limestones, which are oolitic in places, form the lower beds of the D₁ Subzone of the *Dibunophyllum* Zone. A few pseudobreccias are also developed. The Upper D₁ Beds consist of coarse oolites, alternating with thin shales and grits. In the D₂ Subzone the lowest beds show an alternation of grits, limestones and shales. Higher in the section there are grey oolitic limestones, which contain foraminifera, crinoids and corals. The highest beds of the section consist of shales and grits, which are heavily stained with haematite.

The section was sampled at ten-foot intervals, Vaughan's (1906) zonation and description being used as a basis for the collecting. The section sampled was subdivided into nine traverses (Fig. 5). These were as follows:—

1. The riverside traverse of the K Zone. Leigh Woods side of the Gorge. (ST 556 746).

Sample numbers K1–K17.

2. The top of the K Zone and the basal 30' of Z₁ Quarry 1. Leigh Woods side of the Gorge. (ST 557 745).

Samples K18–K21 and Z1–Z10.

3. The Z₁ Limestone traverse in Black Rock Quarry. Clifton side of the Gorge. (ST 561 747).

Sample numbers Z11–Z20.

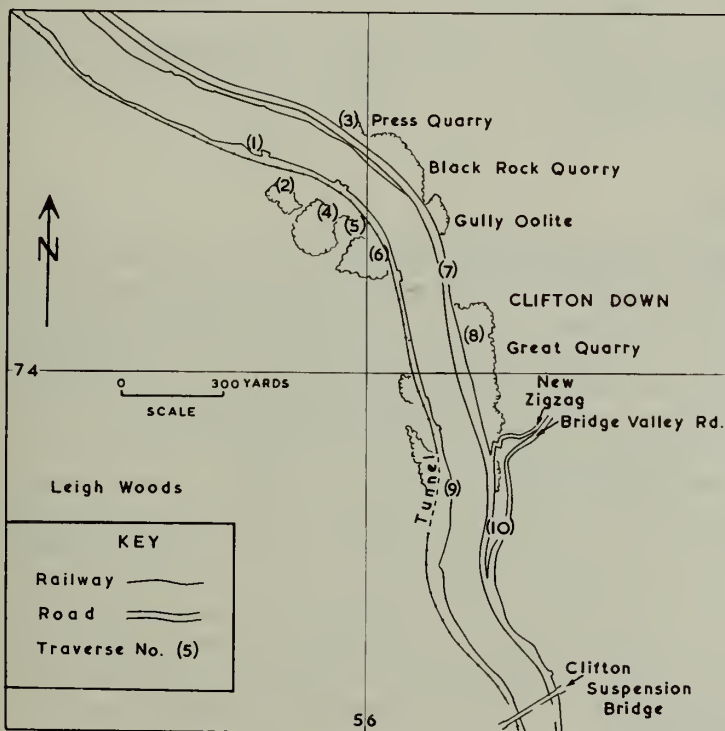


FIG. 5. Sketch map of the Avon Gorge, Bristol, showing localities mentioned in the text.

4. The Z_2 Limestone traverse in Quarry 2. Leigh Woods side of the Gorge. (ST 558 745).
Sample numbers Z21–Z38.
5. The *Laminosa* Dolomite traverse in the Railway cutting, Leigh Woods side of the Gorge, between Quarry 2 and Quarry 3. (ST 559 745).
Sample numbers C1–C11.
6. The *Laminosa* Dolomite and *Caninia* Oolite traverse in Quarry 3. Leigh Woods side of the Gorge. (ST 560 744).
Sample numbers C12–C25.
7. The *Caninia* Dolomite traverse along the roadside on the Clifton side of the Gorge, between the *Caninia* Oolite Quarry to the North and the Great Quarry to the South. (ST 562 746).
Sample numbers C26–C48.
8. The S_1 and lower S_2 traverse in the Great Quarry on the Clifton side of the Gorge. (ST 563 740).
Sample numbers S1–S30.
9. The S_2 and Concretionary Bed riverside traverse, south of Quarry 4. Leigh Woods side of the Gorge. (ST 562 737).
Sample numbers S31–S72.
10. The D Zone traverse at the roadside, north of and a short distance to the south of Bridge Valley Road on the Clifton side of the Gorge. (ST 564 734).
Sample numbers D1–D27.

(ii) South Wales

Rocks of Lower Carboniferous age form an extensive rim around the margins of the South Wales Coalfield, where they overstep the Old Red Sandstone. The thickest and most complete sequence is developed on the southern margin of the Coalfield in Pembrokeshire, Gower and the Vale of Glamorgan. The application of Vaughan's zonal scheme has shown that in this area the complete succession is present, the total thickness being in excess of 4,000 ft. in parts of Pembrokeshire and some 3,500 ft. in Gower, but thinning gradually eastwards. There is a broadly comparable lithological sequence to that of the Bristol area, comprising a lower limestone and shale sequence, followed by bioclastic limestones and oolites, but including varying developments of shales and pseudobreccias in the highest parts, and dolomites in the C and Z Zones in the east. On the North Crop of the coalfield the thickness is much reduced, however, partly as a result of original depositional thinning against the margins of a northerly landmass, partly because of intra-Avonian unconformities, and partly because of truncation below the transgressive unconformable base of the overlying Millstone Grit. The intra-Avonian unconformity cuts out much of the C and S Zones in places.

Our collections were made chiefly from the North Crop of the Coalfield, though

smaller collections were also made from Gower and Pembrokeshire. Detailed descriptions of the local stratigraphy have been given by George (1927 and 1954), Dixey & Sibly (1918) and Owen & Jones (1955). Pringle & George (1961) have reviewed the regional stratigraphy.

Detailed localities and measured sections are given in Figs 59–92 (p. 246), and it is necessary here to give only a brief introduction to the local succession. The youngest strata of the Avonian, the D₃ Upper *Dibunophyllum* Zone, or Upper Limestone Shale, are often cut out by Namurian overstep. The succession was collected by us at Mellte Bridge, at the confluence of the Rivers Mellte and Sychryd, near Craig-y-Dinas (SN 911079 : see Owen & Jones 1955) where it consists of 23 ft. of dark shales and interbedded muddy, and rarely crystalline, crinoidal limestones, most of them less than a foot in thickness. The samples yielded over 3,900 identifiable specimens, whereas beds of similar age from the Black Lias Quarry at The Mumbles, Glamorgan (SS 615883) proved virtually barren in conodonts.

The underlying D₂ Beds were first collected from exposures in the valley of the River Nedd (SN 912122) but these proved to be unfossiliferous, and further collections were made from Craig-y-Dinas (SN 911099) where some 64 ft. of strata are exposed. These consist of massive crystalline limestones with thin interbedded shales. Near the top of the section a thin irregular band of rolled fish fragments and conodonts occurs. The samples yielded over 130 specimens.

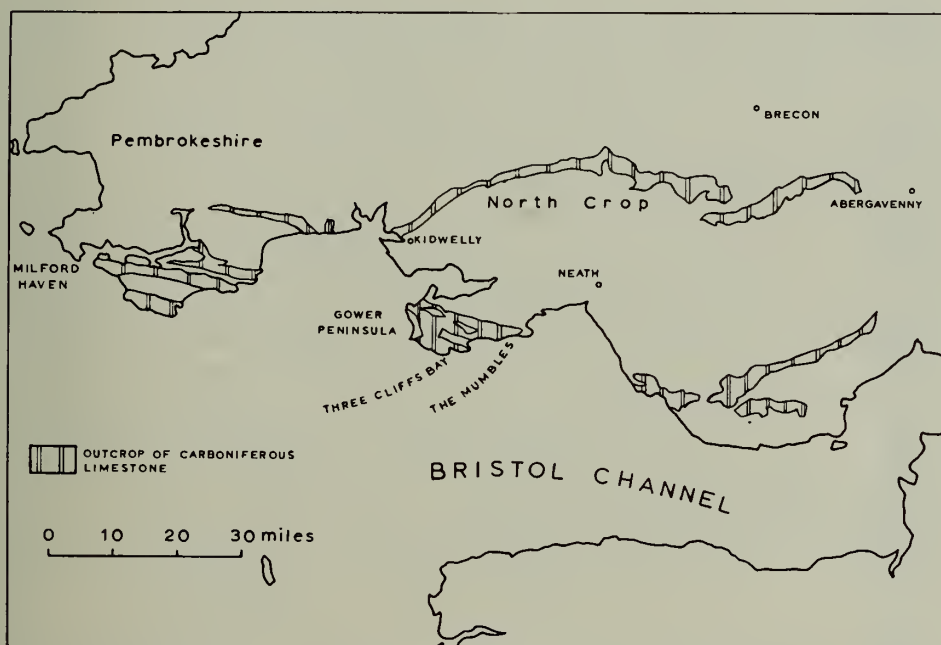


FIG. 6. Map of South Wales to show the main outcrop of the Carboniferous Limestone.

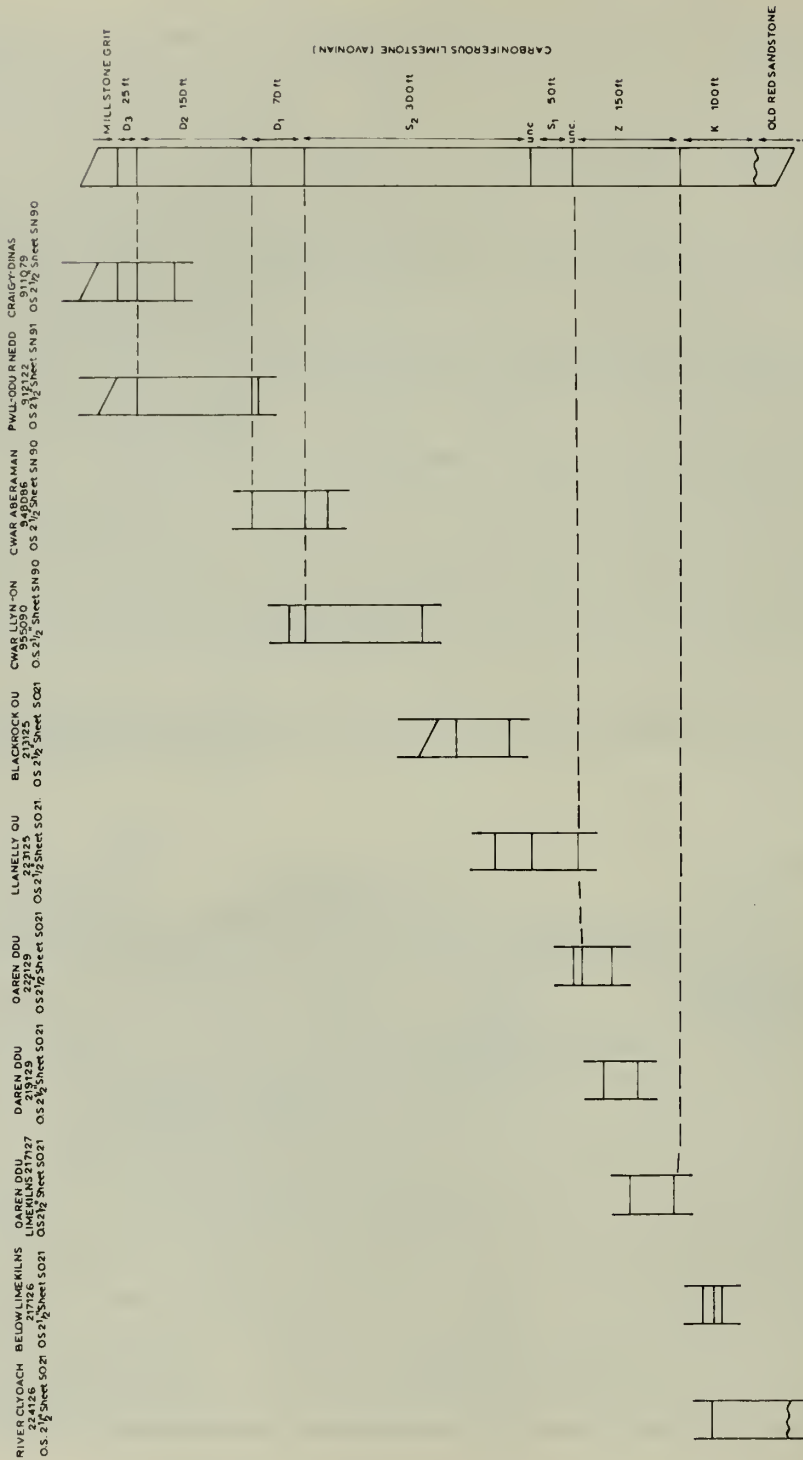


Fig. 7. Generalised sections of Avonian localities on the North Cropp of the South Wales Coalfield, showing the relationships of individual outcrops to the composite section.

These beds overlie some 80 ft. of massive crystalline limestones, which are assigned to the D₁ Subzone. Near the top a "honeycomb" is developed. These samples yielded no conodonts, and the underlying 300 ft. of S₂ grey crystalline limestone also proved barren.

The S₂ and C₂S₁ Zones were collected at Llanelli Quarry (SO 223125), the S₂ comprising over 300 ft. of dolomitic, sandy, massive bedded limestones with occasional brachiopod lenses. The C₂S₁ section consists of about 50 ft. of porcellanous, compact calcite-mudstones with some oolites and green shales (George 1954). None of the samples from these exposures yielded conodonts.

The underlying Z Zone was collected at Blackrock (SO 213125) and consists of 190 ft. of alternating oolites and sugary dolomites, with occasional thin shale bands. All samples in this section yielded conodonts, although some samples yielded only unidentifiable fragments. Over 5,000 specimens were recovered.

The K Zone was collected in the banks of the River Clydach (SO 224126) and along the Heads of the Valleys Road (SO 225130), the contacts with the underlying red sandstone, referred to the Devonian, and the overlying Z Zone both being exposed. The unit consists of alternating calcarenite and shale bands, which range in thickness from 40 ft. to six inches. The limestone samples all yielded conodonts but the shales were unproductive.

(iii) Shropshire

Rocks of Lower Carboniferous age are rare in Shropshire, most of which was emergent during early Carboniferous times. Strata of Lower Carboniferous age, which outcrop on the northern and southern flanks of Titterstone Cleve Hill, are also found at Little Wenlock and Lilleshall. Our collections were made at Farlow (SO 642808), on the northern slopes of Titterstone Cleve Hill, where conglomerates and overlying limestones and shales of the K Zone are well exposed. The basal conglomerate, which reaches a thickness of some 40 ft. in places (Ball & Dineley 1961), overlies Grey Farlow Sandstones of the Upper Old Red Sandstone. The K Zone is overlain by Z Zone oolitic limestones, which are well exposed at Oreton (SO 648806). The overlying Cornbrook Sandstone, once regarded as representing the *Caninia* Zone, has been shown by Jones & Owen (1961) to be of Westphalian age. In contrast, the youngest Lower Carboniferous strata of the Little Wenlock area represent the *Dibunophyllum* Zone.

The Z Zone was collected at Oreton Quarry (SO 648806) where it consists of 20 ft. of pale cream calcarenite, which yielded abundant conodonts.

The underlying K Zone was collected in Farlow Lane (SO 642808), the contact between the zones being unexposed. The K Zone consists of alternating shales and limestones; the lower shales contain quartz pebbles, and lie directly above conglomerates referred to the Old Red Sandstone (Farlovian). Conodonts were recovered from all samples.

(iv) Yorkshire

The Yoredale Formation (Yoredale Series of Phillips 1836) is a succession of

cyclothem typically developed in north-eastern England. In the type area on the Askrigg Block it overlies the Great Scar Limestone and is overlain by the Millstone Grit. The upper contact is partly conformable, partly unconformable; the lower contact is an interdigitation. The typical cyclothem of the Yoredale Formation comprises a thick marine limestone overlain by shale, which is in turn succeeded by sandstone (Moore 1958, Walker 1964). The limestones resemble those of the Great Scar Limestone and the southward failure of the shales and sandstones results in a diachronous (interdigitating) contact between the Yoredale Formation and the Great Scar Limestone, obliterating at least three cyclothem. In Northumberland and Durham the interdigitation occurs at lower and lower levels within the Great Scar Limestone (here called the Melmerby Scar Limestone). The top of the Yoredale Formation extends higher than on the Askrigg Block in consequence of the occurrence of limestones and the non-occurrence of the typical coarse pebbly sandstones of the Millstone Grit, in the generally cyclothem sequence. In terms of the goniatite zones, the Yoredale Formation varies in age as follows:—

Teesdale		early B ₂ to R _{1b}
Wensleydale	(=Yoredale)	late B ₂ to E _{1b}
Grassington		P _{1c} only

The succession in the type area of the Yoredale Formation in Upper Wensleydale is complex, the major cyclothem between two successive thick limestones often including minor rhythms, which possess characters of the typical rhythmic unit, except for the persistence of the limestone (Phillips 1836, Moore 1958, Walker 1964). The succession (Moore 1958 : 94) is as follows:—

- IX Main Limestone
- VIII Underset Limestone
- VII Three Yard Limestone
- VI B
- VI A
- VI Five Yard Limestone
- V A
- V Middle Limestone
- IV C
- IV B
- IV A
- IV Simonstone Limestone
- III C
- III B
- III A
- III Hardraw Scar Limestone
- II Gayle Limestone
- I Hawes Limestone

Names have not been applied to the thin impersistent limestones, which are designated by an index number, indicating the major cyclothem to which they belong, and by an index letter, showing their position in the cyclothem.

Moore (1958 : 95) described the major limestone at the base of the cyclothem and grouped the other beds of the cyclothem together under the term "Non-Calcareous Measures" (although they sometimes contain thin limestones and calcareous shales).

The lower boundary of the Yoredale Formation in the type area was placed by Moore at the base of a thin sandstone-shale sequence, the Thorny Force Sandstone, which lies below the Hawes Limestone. As pointed out by Walker (1964 : 210) this lowest cyclothem is poorly exposed and is confined to a small geographical area. The *Girvanella* Bed, which is accepted as the D₁-D₂ boundary and hence roughly as the B₂-P_{1a} boundary of the goniatite sequence, in the middle of the Hawes Limestone, is in this study taken as the base of the Yoredale Formation.

The Hawes Limestone, which is forty feet thick, may be divided into two distinct members, a lower group of pale grey massive limestones, with pseudobreccias and a fauna of compound corals, and an upper group of blue-grey thinly bedded limestones with few fossils. The boundary between the two is the *Girvanella* Bed, which lithologically is part of the upper group.

The Gayle Limestone, fifty-seven feet thick, may be divided into three parts. At the base is a group of wavy-bedded limestones with irregular shale partings. A massive bed, comparable in thickness to the whole of the underlying thin beds, forms the middle group. The upper part of the Gayle Limestone consists of massively-bedded, blue-grey, poorly-fossiliferous limestones.

The Hardraw Scar Limestone, twenty-five feet thick, consists in the lower half of massive crinoidal limestones, often six feet thick at the base, which pass upwards into thinly-bedded, calcite mudstones. The upper part of the Hardraw Scar Limestone is more uniform than the lower, consisting of massive crinoidal limestones with partings of rubbly limestone, which pass up into finer-grained limestones and fine-grained calcite mudstones, which are partially dolomitised.

Limestone III A is a fine-grained limestone containing corals (*Lithostrotion*). Limestone III B is arenaceous and almost unfossiliferous, whereas Limestone III C is less sandy and contains small crinoids.

The Simonstone Limestone, which is fifteen feet thick, consists in the lower part of a clastic limestone phase, with the development of coarse crinoidal limestones and sandy limestones with a sporadic fauna at the base, which passes upwards into a fine grained limestone and calcareous shale facies which often contains compound corals. The upper part of the Simonstone Limestone consists of fine grained limestone at the base, overlain in turn by coarsely crinoidal limestones and fine grained algal limestones.

Limestone IV A, three feet thick, is a fine grained limestone, which is sandy at the base. Limestone IV B is a fine grained argillaceous limestone, 2½ feet thick, with a 9" bed of shale in the middle.

The Middle Limestone, 65 feet thick, is divisible into three thick limestone units, each separated by shales and thin limestone bands.

The Five Yard Limestone, two feet thick, consists of fine grained limestones, sparingly crinoidal, but with a rich fauna of corals and brachiopods. This formation

is usually developed in two beds with a parting of calcareous shale which has an abundant fauna.

The Three Yard Limestone, which is eight feet thick, is a crinoidal fine grained limestone.

Walker (1964 : 210) suggested that since a continuously exposed section through the whole Yoredale Formation did not exist in the type area, two sections, one representing the upper part and the other the lower part of the Formation, should be taken as type sections. Although Walker's section exposes the beds of his redefined Yoredale Series, it does not include the lower beds of the Yoredale Formation (as defined by Moore 1958). Walker described the upper part of the Formation, from the base of the Hardraw Scar Limestone to the top of the Underset Limestone, as exposed in Long Sike and North Scar Gill at the head of Snaizholme Valley (SD/815840) which is west of the town of Hawes. The lower part of the Formation, from the base of the Hawes Limestone to the base of the Hardraw Scar Limestone, outcrops $3\frac{1}{2}$ miles towards the north east in Gayle Beck (SD/864883), which is near the town of Hawes. The Hardraw Scar Limestone, according to Walker, forms a topographic feature, which can be traced from the base of the first section to the top of the second, and this establishes the relative stratigraphic position of the two sections.

In order to apply the conodont zonation established in south west England to northern England, fifteen samples, one or more being taken from each of the main limestones at the above localities, were processed.

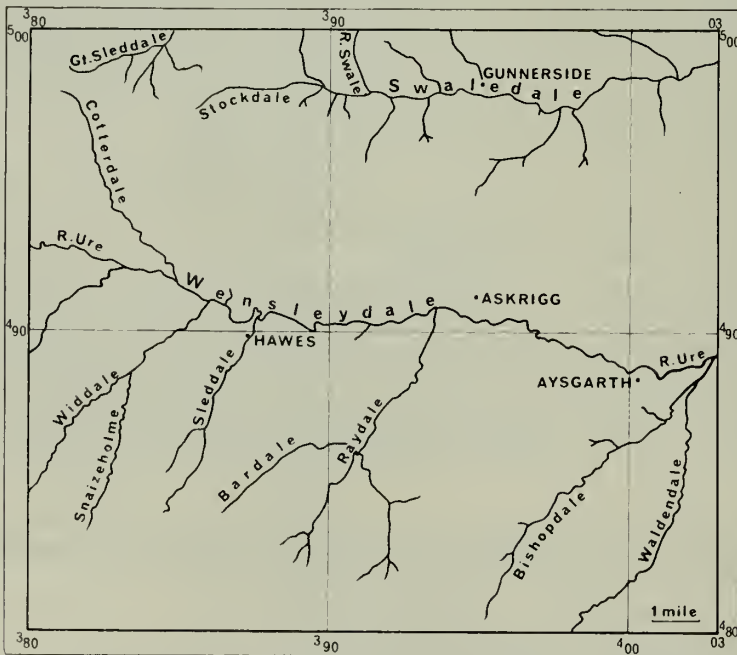


FIG. 8. Outline map of the Wensleydale area, North Yorkshire, from which the Yoredale succession was collected.

(v) Scotland

Rocks of Carboniferous age outcrop over much of the Midland Valley of Scotland. Strata of "Lower" Carboniferous age lie below the Passage Group and Productive Coal Measures of the typical coalfield areas, but in places both the Passage Group and the Oil Shale Groups are replaced by contemporaneous lavas, chiefly of olivine basaltic composition.

These strata were traditionally subdivided into two broad lithological series, the Calciferous Sandstone Series and an overlying Carboniferous Limestone Series. The lower of these divisions is now termed the Calciferous Sandstone Measures, and the upper division is no longer used on maps of the Geological Survey (MacGregor 1960). The lowest division of the Calciferous Sandstone Measures, the Cementstone Group, consists of alternating fine-grained dolomite and shales, whilst the overlying Lower and Upper Shale Groups consist of alternating series of sandstones, shales, coals, fireclays and limestones. Both marine and fresh-water limestones occur and oil shales are widespread. The greatest thickness of the Groups is in the East Fife Coalfield where some 4,000 ft. of strata occur.

The overlying strata (the "Carboniferous Limestone Series" of earlier authors) are subdivided into three lithological groups, the Lower Limestone Group, the Limestone Coal Group, and the Upper Limestone Group. The two higher groups each have a maximum thickness of some 1,500 ft. in the West Fife Coalfield, while the maximum thickness of the Lower Limestone Group is only some 700 ft. Like the Calciferous Sandstone Measures, the whole Carboniferous Limestone "Series" thins rapidly southwestwards into the North Ayrshire Coalfield, where it is reduced in places to less than 100 ft. The Lower Limestone Group consists of thin marine



FIG. 9. Outline map of Southern Scotland, showing localities mentioned in the text.

limestones, including the Hosie Limestones, and inter-bedded shales, with subordinate ironstone nodules and coals. Alternating sandstones, shales, fireclays, and workable coals and ironstones mark the Limestone Coal Group, while the Upper Limestone Group consists predominantly of sandstone, with subordinate shales, limestones and coals.

I. *Dunbar*. Samples were collected from limestone bands within the Lower Limestone Group near Catcraig (NT 715772). The beds collected were the Long Craig Upper (NT 749752), Skateraw Lower (NT 748752), Skateraw Middle (NT 743754), Skateraw Upper (NT 738758), Chapel Point (NT 722774), Barness East (NT 724773) and the Dryburn Foot (NT 732763) Limestones.

II. *Midlothian*. The Lower Limestone Group was collected from various points in the Midlothian Coalfield. The "Gilmerton" Limestone was collected $1\frac{1}{2}$ miles S.S.E. of Carlops (NT 172544) where it consists of grey crystalline limestone and shales, with a limestone breccia at the top. The North Greens Limestone was collected in Bilston Burn (NT 270649) and in the banks of the River North Esk, 250 yds. S.W. of Newhall House. It consists of about 35 ft. of impure, thinly-bedded, argillaceous limestone.

The Vexhim Limestones were collected in Glencorse Burn, 350 yds. upstream from Milston Bridge (NT 250628).

The overlying Bilston Burn Limestone was collected in Bilston Burn, where it consists of about 40 ft. of thinly-bedded limestone, with an overlying bed of calcareous shale and a 5 ft. bed of dolomitic limestone.

III. *Fife*. A thick succession of the Calciferous Sandstone Measures and the Lower Limestone Group is exposed (Figs 85, 86) near Pittenweem (NO 548027) on the shore of the Firth of Forth, between Anstruther and Coal Farm. Samples were collected from the limestone and shale beds, the limestones yielding abundant conodonts, whereas the Calciferous Sandstone Measures, apart from three beds (15, 43, 388), were barren.

IV. *Ayrshire*. Sections through the Lower Limestone Group and the Upper Limestone Group were collected.

The Broadstone Limestone was collected at Auchenmade (NS 342486) where it is overlain by the Dockra Limestone, which was also collected here. The Hosie Limestones were collected in a railway cutting at Glengarnock (NS 333525).

In the Upper Limestone Group the Index Limestone was collected near Glonbeith Castle (NS 332458) and near Drumbuie House (NS 361506) where it was about six feet thick.

The Lower and Upper Linn Limestones were collected at the Linn Spout near Dalry (NS 287487, NS 284485).

V. *Roxburghshire*. The Main Algal 'Series' of Garwood (1931) was collected in Harden Burn (NY 517907) and the limestone bands, apart from the algal bed, yielded abundant conodonts.

VI. *Argyll*. The Carboniferous Limestone 'Series' at Machrihanish (McCallien 1928 ; McCallien & Anderson 1930) was examined and the limestones were collected where they were exposed on the beach (NR 632208).

The general geology of the Scottish collecting areas is described in the following publications: Carruthers *et al.* (1927), Clough *et al.* (1925), Craig (1965), Currie (1954), Dinham & Holdane (1932), Goodlet (1957), George (1958), Mitchell & Mykura (1962), Richey *et al.* (1930), Robertson *et al.* (1949) and Tulloch & Walton (1958).

IV. METHODS OF STUDY

Samples were collected from the successions at intervals of 10 ft. and in many parts of the sections these were supplemented by collections made at 5 ft. or 2 ft. intervals. Most of the original samples from the reconnaissance survey weighed about 25 lbs. but the samples from the smaller intervals weighed only 2–4 lbs.

These samples were weighed and then digested in 8% commercial acetic acid, contained in plastic buckets. Shales were disintegrated with concentrated hydrogen peroxide, and formic acid was used for some of the limestones. After the rock had dissolved, the sludge was sieved under water on 25, 50, 100 and 200 mesh screens, the fractions being dried and then separated in bromoform.

The heavy residues were searched with a binocular microscope and the conodonts picked and mounted (see Collinson 1963 for further details).

Photography was carried out by Mr. S. Osborn, using a Leitz Aristophot apparatus and Adox KB 14 film, developed in Acutol or I.D. 48 developer. The specimens were coated with ammonium chloride. Prints were cut out and mounted but no retouching was undertaken.

V. CONODONT FAUNAS

(a) General Review

The present study is based upon 600 rock samples, and has involved the solution of some 3 tons of rock, which yielded over 25,000 identifiable conodonts. We regard this total collection as satisfactory, although the average abundance of conodonts per kilogram of rock is considerably lower than the yields from some other areas.

The distribution of conodonts within the various sections studied was far from uniform, and abundance ratios for each sample are included with each of the lithological sections (Figs 59–92). The succession in the Avon Gorge illustrates the problems involved in the less fossiliferous parts of the section. The average number of conodonts per kilogram was 8 for the K Zone, with a range from 0–47 per kilogram. In general the shales provided poor yields or were barren, while intervening limestones were relatively fossiliferous. Shale samples 7 and 8, for example, were barren, but they are separated by two thin limestones, yielding 20 and 16 conodonts per kilogram.

The Z Zone consists predominantly of massive, blue-grey calcarenite, and has an average yield of 19 conodonts per kilogram. There is again a fair range of variation (0–66 per kg.), the lowest yields being in limestones with a high haematite content. The upper beds of the Zone had high yields (45–66 per kg.).

In contrast, the Lower C₁, the *Laminosa* Dolomite, yielded an average of only 3 conodonts per kilogram, probably reflecting either the destructive results of second-

ary dolomitisation, or possibly an unfavourable depositional environment, while the upper C₁ *Caninia* Oolite had an average yield of only 1 conodont per kilogram (range 0–3 per kg.). Other conodont students have commonly found lithologically similar oolites to have low yields, and this may be the result of relatively rapid deposition. Of the 23 samples of the *Caninia* Dolomite which were processed, only one, a shelly calcarenite, yielded conodonts.

S Zone samples had a yield of less than 1 per kilogram, and almost three quarters of the 72 samples processed were barren. Only 5 samples yielded an average of more than one conodont per kilogram. The Zone is marked by relatively little change in the conodont faunas, and, like the low yielding (1 per kg.) D Zone beds, probably represents rapidly deposited sediments.

Broadly comparable variations in abundance are seen in strata of similar lithologies from other sections. In the D Zone of South Wales, for example, the mean yield was 29 conodonts per kilogram of limestone dissolved, with a range from 0–198. In the Z Zone of the North Crop, the mean yield was 9 conodonts per kilogram, with a range from 0–60. In general the lowest yields were those of the saccharoidal dolomites, and the highest were those of the basal beds of oolites.

(b) Stratigraphical distribution of conodont faunas

The precise ranges of all conodont species recovered for each of the various areas are shown on Figs. 49–58. The present section provides only a general view of the distribution of some of the more useful genera and species.

Patrognathus gen. nov. is restricted to the K Zone. The genus *Clydagnathus* gen. nov. is found in the K Zone and in the lower part of the Z Zone of the North Crop and in Shropshire. It is rare in large faunas of the same age from the Avon Gorge, although it occurs abundantly in some other countries, e.g. Australia. The lowest occurrence of the genus is represented by the species *C. gilwernensis* gen. et sp. nov. and *C. cavusformis* gen. et sp. nov., which are rapidly replaced by *Clydagnathus* sp. A gen. et sp. nov. The Lower Z Zone species are *C. unicornis* gen. et sp. nov. and *C. darensis* gen. et sp. nov. The genus *Siphonodella*, which has proved to be abundant and of great stratigraphical value in other areas, is rare in the Avonian. It is confined to the upper part of the K Zone in both the Avon Gorge and the North Crop. The limited stratigraphic range of the genus in the Avonian is also reflected in an absence of the sequence of species, which has been described from the Mississippi Valley.

The genus *Pseudopolygnathus* is one of the most distinctive components of the faunas of the K and Z Zones, extending from the base of the K Zone into the C₁ *Laminosa* Dolomite. It is represented by a considerable number of species, most of which have restricted stratigraphical ranges. *Pseudopolygnathus vogesi* sp. nov. and *Pseudopolygnathus expansus* sp. nov. are confined to the lowest part of the K Zone, where they are distinctive species. The Z Zone is characterized by the incoming of abundant pseudopolygnathids, referable to the species *P. primus* Branson & Mehl and *P. cf. dentilineatus* E. R. Branson. These are replaced vertically by *P. postinodosus* sp. nov. and *P. nodomarginatus* E. R. Branson. In contrast to the abundance

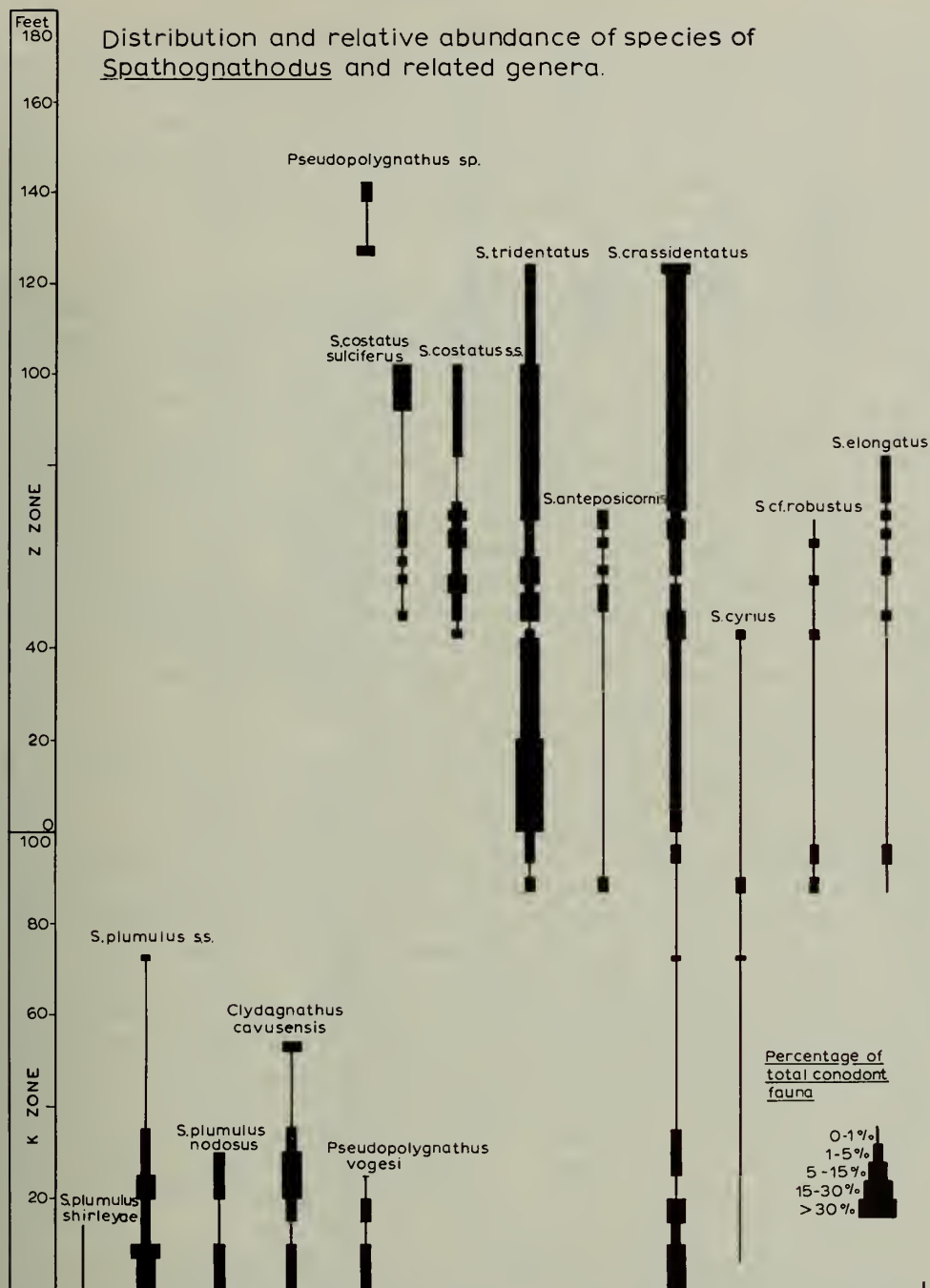


FIG. 10. Distribution and relative abundance of species of *Spathognathodus* and related genera in the Z and K Zones of the Avonian of the North Crop.

of *Pseudopolygnathus* in the Lower Z Zone of the Avon Gorge, the genus is absent in strata of similar age from the North Crop. In these latter faunas it is presumably represented by functional homoeomorphs in the natural conodont assemblages. These could well be spathognathodids, from which *Pseudopolygnathus* seems to have arisen. The Lower Z Zone assemblage is replaced by abundant *P. multistriatus* Mehl & Thomas near the base of the Z₂ Subzone, which is in turn replaced by abundant *P. longiposticus* (Branson & Mehl) towards the top of the Z₂ Subzone. The genus is rare in the Lower C₁ Subzone.

The genus *Gnathodus* is one of the longest ranging in the Avonian, but its restricted and distinctive species have been particularly useful in some of our correlations. Its oldest occurrence is near the base of the Z₂ Subzone, where *G. delicatus* Branson & Mehl is found. On the North Crop, *G. simplicatus* sp. nov. also occurs in Lower Z Zone faunas. *G. delicatus* is associated near the top of the Z₂ Subzone with *G. semiglaber* (Bischoff), a distinctive Upper Z Zone species, which is in turn replaced by *G. antetexanus* Rexroad & Scott at the top of the Z Zone. *G. punctatus* (Cooper), *G. avonensis* sp. nov. and *G. simplicatus* sp. nov. also occur in the Upper Z Zone. A single specimen of *G. cuneiformis* Mehl & Thomas was collected in the middle of the S₁ Subzone. *Gnathodus* is rare or absent in the higher C and S faunas, but is represented by several distinctive species in the D Zone. *G. bilineatus* (Roundy) appears at the base of the D₂ Subzone, together with *G. girtyi girtyi* Hass. In the highest part of the D₂ Subzone *G. girtyi simplex* Dunn, *G. commutatus* (Branson & Mehl), *G. mononodosus* sp. nov. and *G. homopunctatus* Ziegler appear. *G. girtyi collinsoni* sub. sp. nov. appears in the middle of the D₃ Subzone, and *G. girtyi turritus* Collinson & Druce near the top (Fig. 11).

The genus *Spathognathodus* has an extended range, being present throughout the Avonian. The dominant species of the Lower K Zone is *S. plumulus* sp. nov., which is represented by several subspecies. The Upper K Zone is marked by a variety of spathognathodids, including *S. elongatus* (Branson & Mehl), *Spathognathodus* cf. *robustus* (Branson & Mehl), *S. anteposicornis* Scott, and *S. tridentatus* (E. R. Branson). The three former species, though never abundant, extend into the Lower Z Zone, while the latter, together with *S. crassidentatus*, which first appears in the basal K Zone, is abundant in the Lower and Middle Z Zone. *S. costatus costatus* (E. R. Branson) and *S. costatus sulciferus* (Branson & Mehl) appear in the Lower Z Zone in the North Crop and are abundant in the middle part of the Zone. *S. cyrius* (Cooper), a rare species throughout the K and Lower Z Zones, overlaps the lower occurrence of these species, and *S. cf. cristulus* Youngquist & Miller is also present, extending upwards into the C Zone. *S. pulcher* Branson & Mehl occurs high in the Z Zone and *S. coronus* sp. nov. in the C Zone. *S. scitulus* (Hinde) is present in the *Caninia* Oolite and extends into the D Zone. *S. cristulus* Youngquist & Miller is characteristic of the D₂ Subzone and *S. campbelli* Rexroad of the D₃.

Polygnathus first appears near the base of the K Zone and extends to the top of C₁. *Polygnathus communis* Branson & Mehl extends from near the base of the K Zone to the middle of the *Laminosa* Dolomite. *Polygnathus inornatus inornatus* Branson & Mehl, *P. lobatus lobatus* Branson & Mehl, *P. inornatus rostratus* subsp. nov., *P.*

AVONIAN CORAL-BRACHIOPOD ZONES

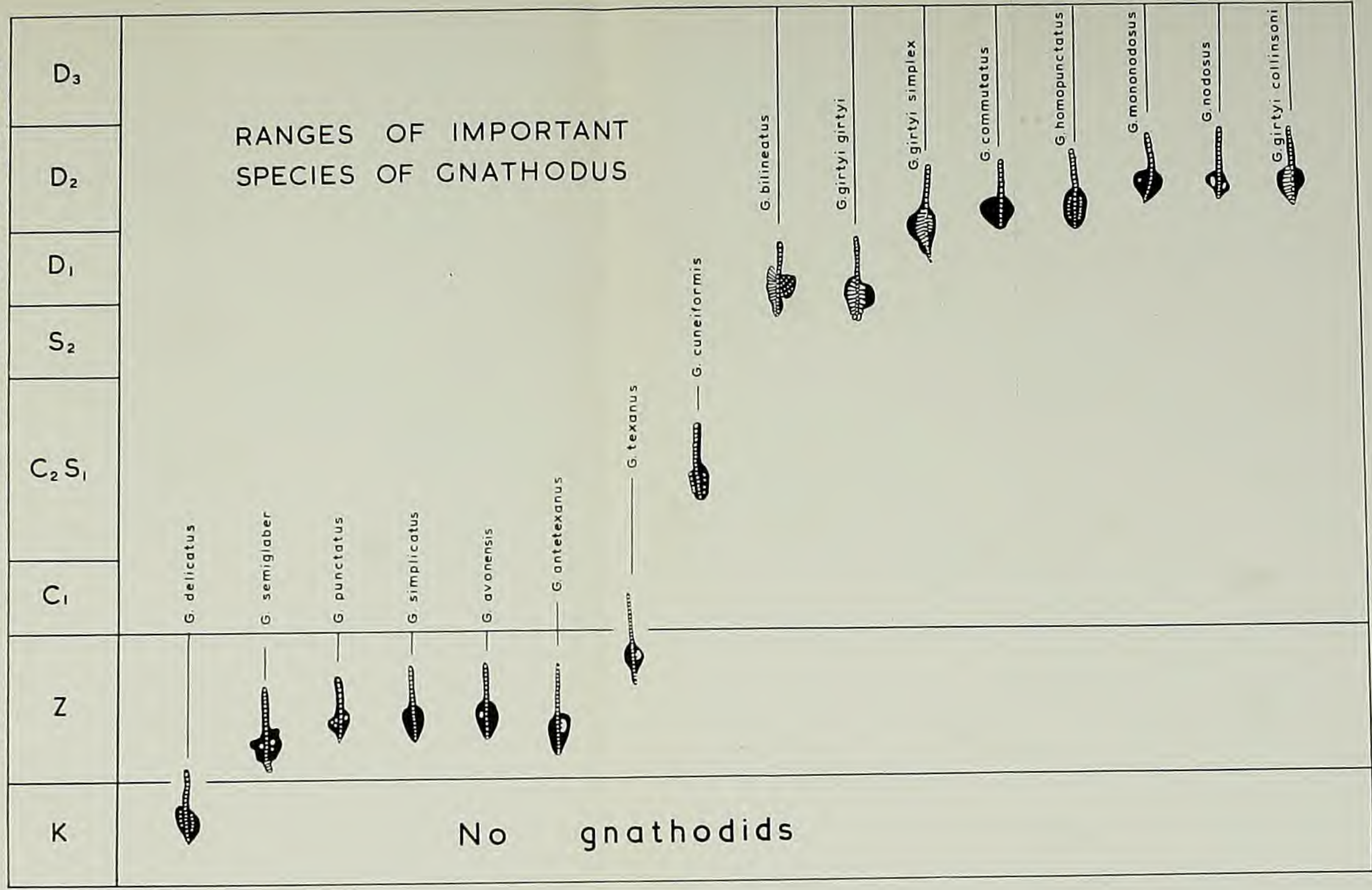


FIG. 11. Ranges of important species of the genus *Gnathodus* in the Avonian.

inornatus vexatus subsp. nov. and *P. lobatus inflexus* subsp. nov. appear in the Middle K Zone. The *P. inornatus* group becomes extinct in the upper part of the K Zone. The *P. lacinatus* Huddle group appears in the uppermost Z Zone, together with *P. lacinatus asymmetricus* subsp. nov. The C Zone is characterized by *P. lacinatus* s.s. and *P. bischoffi* sp. nov.

The genus *Mestognathus* first appears in the upper part of the C₁ Subzone, where it is represented by *M. beckmanni* Bischoff, which extends into the D Zone. *M. bipluti* Higgins first appears in the D₁ Subzone and extends into the higher part of D₂, where *M. neddensis* sp. nov. is also present. Neither extends into the D₃ Subzone.

Cavusgnathus is most characteristic of the C₂, S and D Zones. *C. unicornis* Youngquist & Miller is present in the C₂ Caninia Dolomite and extends into the D Zone. *C. charactus* Rexroad first occurs in the C₂S₁ Zone, and *C. convexus* Rexroad is characteristic of the Middle S Zone.

The genus *Taphrognathus* is restricted to the Upper S₂ Subzone, where it is represented by a single species, *T. varians* Branson & Mehl.

The striking genera *Bactrognathus*, *Doliognathus*, *Scaliognathus* and *Staurognathus*, which are distinctive components of faunas of comparable age in other areas, are unrepresented in our Avonian faunas, in which the genus *Elictognathus* is represented by only a single fractured specimen. It seems probable that these genera were geographically or ecologically restricted.

Most of the genera of "bars and blades" have a long stratigraphic distribution, but a number of species have proved valuable in local correlation. *Ligonodina beata* nom. nov., *Hindeodella corpulenta* Branson & Mehl, and *H. subtilis* Ulrich & Bassler are common Upper K and Z Zone forms. *Apatognathus* makes its first appearance in the Z₂ Subzone. *A. geminus* (Hinde) is present in the C₁ Subzone and extends into the D Zone. *A. scalenus* Varker appears in the Upper C₁ Subzone. *A. bladus* sp. nov. is confined to the D₂ Subzone. *Prioniodina laevipostica* (Rexroad & Collinson) is limited to the Upper D₂ Subzone. *Neoprioniodus scitulus* (Branson & Mehl), *N. peracutus* (Hinde), *Hindeodella undata* Branson & Mehl, and *H. antecomplex* Collinson & Druce first appear in the Lower D₃ Subzone. *Magnilaterella clarkei* sp. nov. is confined to the D Zone, as is *Kladognathus*.

The precise ranges of these and other species are given on Figs. 49-58. The low yield of conodonts from many samples makes reliance upon any single "index fossil" an unreliable method of correlation, but the general characteristics of the individual conodont assemblages are distinctive for each of our main stratigraphic divisions, and these provide the basis of a relatively precise scheme of correlation.

(c) Avonian Conodont Biostratigraphical Zones

A series of 14 conodont assemblage zones has been established. We have used the Avon Gorge and the North Crop successions as our type sections, using the latter to provide the three highest Avonian Zones, which are largely represented by non-carbonate sediments in the Avon Gorge area. We have therefore included in this section a detailed discussion of the correlation between these two areas, in order to provide a basis for the zonal scheme, which we have used (p. 46) to establish correla-

tions between these type sections and Avonian sequences in Central England and Scotland. We believe that these conodont zones provide a useful method of correlation throughout the British Avonian, and that they offer a considerably higher degree of precision than existing coral-brachiopod zones.

They show no detailed correspondence to the conodont zones established in either the Mississippi Valley or in West Germany, although the general faunal sequence in the three areas has enough broad resemblances to allow us to correlate between them with some confidence.

The sequence and relationship of the 14 zones are shown in Fig. 12. They are defined and described below, and the detailed correlation between the Avon Gorge and the North Crop is discussed. The intercontinental correlations given for each zone below are generalized and approximate. There is a full discussion of correlation on p. 52.

Patrognathus variabilis—*Spathognathodus plumulus plumulus* Assemblage Zone

CHARACTERISTIC SPECIES: *Patrognathus variabilis* gen. et sp. nov., *Spathognathodus plumulus plumulus* sp. nov., *Pseudopolygnathus vogesi* sp. nov., *Spathognathodus plumulus shirleyae* sp. et subsp. nov. and, in North Crop, *Clydagnathus gilwernensis* gen. et sp. nov.

LIMITS: The base of the assemblage zone is not identified, but probably corresponds to the first appearance of *P. variabilis* gen. et sp. nov. The upper limit coincides with the oldest stratigraphic occurrence of *Polygnathus inornatus inornatus* Branson & Mehl, *Polygnathus lobatus lobatus* Branson & Mehl, and also of the genus *Siphonodella*.

REMARKS: This zone occupies the lower and middle of the K Zone (Samples K 1–K 11 in the Avon Gorge and Samples KL 1–KL 13 on the North Crop). It is correlated with part of the Cu I of West Germany, the lower and middle parts of the Hannibal Formation of North America and with the Tn_{2b} and Lower Tn_{2c} of Belgium.

The lowest Lower Limestone Shale, which immediately overlies the Old Red Sandstone in the Avon Gorge, does not contain conodonts. The basal limestone stratum (Sample K 3) is characterized by the presence of *S. plumulus plumulus* subsp. nov. and *P. variabilis* gen. et sp. nov. Sample K 4 is the oldest from the Avon Gorge to contain pseudopolygnathids, whereas these pseudopolygnathids occur in the North Crop in the basal beds of the Lower Limestone Shale which directly overlies the Old Red Sandstone.

FIG. 13. Chart to show the characteristic species of the conodont zones proposed in the present paper. Where a species is shown breaking the boundary between two successive zones, it is present in both.

Patrognathus variabilis—*Spathognathodus plumulus plumulus* Assemblage Zone. 1a. *Patrognathus variabilis* gen. et sp. nov.—oral view. 1b. *Patrognathus variabilis* gen. et sp. nov.—lateral view. 2a. *Spathognathodus plumulus plumulus* sp. nov.—lateral view. 2b. *Spathognathodus plumulus plumulus* sp. nov.—oral view. 3a. *Pseudopolygnathus vogesi* sp. nov.—oral view. 3b. *Pseudopolygnathus vogesi* sp. nov.—aboral view. 4a. *Spathognathodus plumulus shirleyae* subsp. nov.—lateral view. 4b. *Spathognathodus*

NORTH AMERICAN SERIES	MISSISSIPPI VALLEY FORMATIONS.	MISSISSIPPI VALLEY CONODONT ZONES.	EUROPEAN ZONES	AVONIAN CONODONT ZONES	SAMPLE NUMBERS	CORAL BRACHIOPOD ZONES
CHESTERIAN	GLEN DEAN	<i>Gnathodus bilineatus</i> - <i>Kladagnathodus mehli</i>	E1	<i>Gnathodus girtyi collinsoni</i>	Y0	D ₃
	HARDINSBURG GOLCONDA CYPRESS RIDENHOWER	<i>Gnathodus bilineatus</i> - <i>Cavusgnathus cristatus</i>	Cu III Y		Y27	
	BETHEL DOWNEY'S BLUFF TANNECTOWN REHAULT AUX. 14568	<i>Gnathodus bilineatus</i> - <i>Cavusgnathus charactus</i>			308=Y28	
VALMEYERAN	ST. GENEVIEVE		Cu III A	<i>Gnathodus monanodasus</i>	307	D ₂
					CY07	
	ST. LOUIS	<i>Apatagnathus geminus</i> - <i>Cavusgnathus</i>	Cu III B	<i>Mestagnathus beckmanni</i> - <i>Gnathodus bilineatus</i>	CY06	D ₁
					CY01	
	SALEM	<i>Taphragnathus varians</i> - <i>Apatagnathus</i> ?	Cu III B	<i>Apatagnathus geminus</i> - <i>Cavusgnathus</i>	D9	S ₂
					S59	
	WARSAW		Cu III B	<i>Taphragnathus varians</i> - <i>Cavusgnathus</i> - <i>Apatagnathus</i>	S58	S ₂
	KEOKUK	<i>Gnathodus texanus</i> - <i>Taphragnathus</i>		No Conodonts	S45	
	UPPER BURLINGTON	<i>Bactragnathus</i> - <i>Taphragnathus</i>	Cu III B	<i>Cavusgnathus unicornis</i> - <i>Apatagnathus</i>	S44	C ₂ S ₁
	MIDDLE AND LOWER BURLINGTON			No Conodonts	C39	
	FERN GLEN	<i>Bactragnathus</i> - <i>Polygnathus communis</i>	Cu III B	<i>Mestagnathus beckmanni</i> - <i>Polygnathus bischoffi</i>	C38	C ₁
	"SEDALIA" ? ? ? ? UNCONFORMITY ?	<i>Gnathodus semiglaber</i> - <i>Pseudopolygnathus multistriatus</i>		<i>Mestagnathus beckmanni</i> - <i>Polygnathus bischoffi</i>	C25	
	UPPER CHOUTEAU	<i>Siphonodella isosticha</i> - <i>S. cooperi</i>	Cu III A-Y	<i>Gnathodus antetexanus</i> - <i>Polygnathus lacinatus</i>	C15	C ₁
LOWER CHOUTEAU		<i>Gnathodus antetexanus</i> - <i>Polygnathus lacinatus</i>		C14		
UPPER HANNIBAL	<i>Siphonodella quadruplicata</i> - <i>S. crenulata</i>	Cu III A-Y	<i>Polygnathus lacinatus</i> <i>Pseudopolygnathus</i> cf. <i>P. longiposticus</i>	C1	Z	
MIDDLE HANNIBAL	<i>Siphonodella duplicata</i>		<i>Polygnathus lacinatus</i>	Z38		
LOWER HANNIBAL	<i>Siphonodella sulcata</i>	Cu III A-Y	<i>Polygnathus lacinatus</i>	Z33	Z	
			<i>Polygnathus lacinatus</i>	Z32		
KINDERHOOKIAN	UPPER CHOUTEAU	<i>Siphonodella isosticha</i> - <i>S. cooperi</i>	Cu II X	<i>Spathognathodus costatus costatus</i> - <i>Gnathodus delicatus</i>	Z25	K
	LOWER CHOUTEAU			<i>Spathognathodus costatus costatus</i> - <i>Gnathodus delicatus</i>	K19	
	UPPER HANNIBAL	<i>Siphonodella quadruplicata</i> - <i>S. crenulata</i>	<i>Spathognathodus</i> cf. <i>S. robustus</i> - <i>S. tridentatus</i>	K18		
	MIDDLE HANNIBAL	<i>Siphonodella duplicata</i>	<i>Siphonodella</i> - <i>Polygnathus inornatus</i>	K ₂₁ KL19 KL18		
	LOWER HANNIBAL	<i>Siphonodella sulcata</i>	<i>Patragnathus variabilis</i> - <i>Spathognathodus plumulus</i>	K12		
		Cu I	<i>Patragnathus variabilis</i> - <i>Spathognathodus plumulus</i>	K11	K	
				K1		

FIG. 12. Zonation of the Avonian on the basis of conodonts, showing the relationship of the zones proposed in this paper to the coral/brachiopod divisions of the Avon Gorge, and the North Crop, and also the relationship of the Yoredale strata in the upper part of the succession. A comparison is made with the conodont zones established in the Mississippi Valley and with the goniatite zones of Europe.

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CORAL BRACHIOPOD ZONES	CONODONT ZONES	CHARACTERISTIC SPECIES
D ₃	<i>Gnathodus girlyi collinsoni</i>	
D ₂	<i>Gnathodus monododus</i>	
D ₁	<i>Mesognathus beckmanni</i> - <i>Gnathodus bilineatus</i>	
S ₂	<i>Apotognathus</i> <i>Cavagnathus</i>	
C ₂ S ₁	NO CONODONTS	
C ₁	<i>Mesognathus beckmanni</i> - <i>Polygnathus bischoffi</i>	
Z	<i>Gnathodus antilexanus</i> <i>Polygnathus lacinatus</i>	
Z	<i>Spathognathus costatus costatus</i> - <i>Gnathodus delicatus</i>	
K	<i>Spathognathodus cf. S. robustus</i> - <i>S. tridentatus</i>	
K	<i>Siphonodella</i> - <i>Polygnathus inornata</i>	
K	<i>Patragnathus variabilis</i> - <i>Spathognathodus plumulus</i>	

FIG. 13.

plumulus shirleyae subsp. nov.—oral view. 5a. *Clydagnathus gilwernensis* gen. et sp. nov.—oral view. 5b. *Clydagnathus gilwernensis* gen. et sp. nov.—lateral view.

Siphonodella—*Polygnathus inornatus* Assemblage Zone. 6a. *Polygnathus inornatus inornatus*—lateral view. 6b. *Polygnathus inornatus inornatus*—oral view. 7a. *Polygnathus lobatus lobatus*—oral view. 8. *Polygnathus lobatus inflexus*—oral view. 9a. *Polygnathus inornatus rostratus*—oral view. 9b. *Polygnathus inornatus rostratus*—aboral view. 10a. *Siphonodella isosticha*—aboral view. 10b. *Siphonodella isosticha*—oral view.

Spathognathodus cf. *robustus*—*S. tridentatus* Assemblage Zone. 11. *Spathognathodus* cf. *robustus*—lateral view. 12. *Spathognathodus elongatus*—lateral view. 13a. *Spathognathodus tridentatus*—lateral view. 13b. *Spathognathodus tridentatus*—oral view. 13c. *Spathognathodus tridentatus*—aboral view. 14. *Spathognathodus crassidentatus*—lateral view. 15. *Spathognathodus anteposicornis*—lateral view.

Spathognathodus costatus costatus—*Gnathodus delicatus* Assemblage Zone. 16a. *Spathognathodus costatus costatus*—lateral view. 16b. *Spathognathodus costatus costatus*—aboral view. 17a. *Spathognathodus costatus sulciferus*—lateral view. 17b. *Spathognathodus costatus sulciferus*—oral view. 18a. *Spathognathodus* cf. *crisulus*—lateral view. 18b. *Spathognathodus* cf. *crisulus*—oral view. 19. *Spathognathodus* cf. *cyrius*—lateral view. 20a. *Gnathodus delicatus*—lateral view. 20b. *Gnathodus delicatus*—oral view. 21. *Ligonodina beata* nom. nov.—inner lateral view. 22. *Hindeodella corpulenta*—lateral view. 23. *Hindeodella subtilis*—lateral view. 24a. *Pseudopolygnathus primus*—oral view. 24b. *Pseudopolygnathus primus*—aboral view. 25. *Pseudopolygnathus* cf. *dentilineatus*—oral view. 26a. *Pseudopolygnathus multistriatus*—aboral view. 26b. *Pseudopolygnathus multistriatus*—oral view. 27. *Gnathodus simplicatus* sp. nov.—oral view. 28a. *Clydagnathus unicornis* gen. et sp. nov.—oral view. 28b. *Clydagnathus unicornis* gen. et sp. nov.—lateral view. 29a. *Pseudopolygnathus postinodosus* sp. nov.—oral view. 29b. *Pseudopolygnathus postinodosus* sp. nov.—lateral view.

Polygnathus lacinatus Assemblage Zone. 30. *Polygnathus lacinatus lacinatus*—oral view. 31a. *Polygnathus lacinatus asymmetricus* subsp. nov.—lateral view. 31b. *Polygnathus lacinatus asymmetricus* subsp. nov.—oral view. 32. *Polygnathus nodomarginatus*—oral view. 33a. *Cavusgnathus* sp. nov. A.—oral view. 33b. *Cavusgnathus* sp. nov. A.—lateral view. 34. *Pseudopolygnathus multistriatus*—oral view.

Polygnathus lacinatus—*Pseudopolygnathus* cf. *P. longiposticus* Assemblage Zone. 35. *Gnathodus semiglaber*—oral view. 36a. *Gnathodus delicatus*—lateral view. 36b. *Gnathodus delicatus*—oral view. 37. *P.* cf. *longiposticus*—lateral view. 38. *Polygnathus lacinatus lacinatus*—oral view. 39a. *Spathognathodus pulcher*—oral view. 39b. *Spathognathodus pulcher*—lateral view. 40. *Gnathodus simplicatus* sp. nov.—oral view. 41a. *Gnathodus avonensis* sp. nov.—oral view. 41b. *Gnathodus avonensis* sp. nov.—lateral view.

Gnathodus antetexanus—*Polygnathus lacinatus* Assemblage Zone. 42. *Apatognathus geminus*—inner lateral view. 43. *Apatognathus scalenus*—inner lateral view. 44. *Apatognathus petilus*—outer lateral view. 45a. *Spathognathodus* cf. *crisulus*—lateral view. 45b. *Spathognathodus* cf. *crisulus*—oral view. 46. *Gnathodus antetexanus*—oral view.

Mestognathus beckmanni—*Polygnathus bischoffi* Assemblage Zone. 47a. *Mestognathus beckmanni*—lateral view. 47b. *Mestognathus beckmanni*—oral view. 48a. *Polygnathus bischoffi* sp. nov.—oral view. 48b. *Polygnathus bischoffi* sp. nov.—aboral view.

Cavusgnathus unicornis—*Apatognathus* Assemblage Zone. 49. *Cavusgnathus unicornis*—inner lateral view. 50a. *Spathognathodus crisulus*—lateral view. 50b. *Spathognathodus crisulus*—oral view. 51a. *Mestognathus beckmanni*—inner lateral view. 51b. *Mestognathus beckmanni*—oral view. 52a. *Gnathodus cuneiformis*—oral view. 52b. *Gnathodus cuneiformis*—lateral view. 53a. *Cavusgnathus charactus*—oral view. 53b.

In addition, on the North Crop two subzones can be delineated, the lower being characterized by the presence of *Spathognathodus plumulus nodosus* sp. et subsp. nov., *Clydagnathus gilwernensis* gen. et sp. nov. and *Pseudopolygnathus vogesi* sp. nov. The upper is recognized by the absence of the above-mentioned species and by the presence of *Clydagnathus* sp. nov. A.

Siphonodella—*Polygnathus inornatus* Assemblage Zone

CHARACTERISTIC SPECIES: *Polygnathus inornatus inornatus* Branson & Mehl, *Polygnathus lobatus lobatus* Branson & Mehl, *Polygnathus lobatus inflexus* subsp. nov., *Polygnathus inornatus rostratus* subsp. nov. and *Siphonodella isosticha* (Cooper).

LIMITS: The base of this zone is marked by the first occurrence of *Siphonodella isosticha* (Cooper), *P. inornatus inornatus* Branson & Mehl, *P. lobatus lobatus* Branson & Mehl, and *P. inornatus rostratus* subsp. nov. The top of the zone is marked by the

Continuation of Fig. 13 caption]

Cavusgnathus charactus—inner lateral view. 54a. *Cavusgnathus cristatus*—inner lateral view. 54b. *Cavusgnathus cristatus*—oral view.

Taphrognathus varians—*Cavusgnathus*—*Apatognathus* Assemblage Zone. 55a. *Taphrognathus varians*—oral view. 55b. *Taphrognathus varians*—lateral view. 56a. *Spathognathodus cristulus*—oral view. 56b. *Spathognathodus cristulus*—lateral view.

Apatognathus ? *geminus*—*Cavusgnathus* Assemblage Zone. 57a. *Cavusgnathus cristatus*—inner lateral view. 57b. *Cavusgnathus cristatus*—oral view. 58. *Apatognathus* ? *geminus*—inner lateral view.

Mestognathus beckmanni—*Gnathodus bilineatus* Assemblage Zone. 59a. *Mestognathus beckmanni*—inner lateral view. 59b. *Mestognathus beckmanni*—oral view. 60. *Cavusgnathus unicornis*—inner lateral view. 61. *Spathognathodus scitulus*—lateral view. 62a. *Apatognathus bladus* sp. nov.—inner lateral view. 62b. *Apatognathus bladus* sp. nov.—outer lateral view. 63. *Hibbardella abnormis*—inner lateral view. 64. *Neoprioniodus singularis*—lateral view. 65a. *Gnathodus girtyi girtyi*—oral view. 65b. *Gnathodus girtyi girtyi*—lateral view. 66a. *Gnathodus bilineatus*—oral view. 66b. *Gnathodus bilineatus*—lateral view.

Gnathodus mononodosus Assemblage Zone. 67a. *Gnathodus girtyi simplex*—lateral view. 67b. *Gnathodus girtyi simplex*—oral view. 68a. *Gnathodus mononodosus* sp. nov.—lateral view. 68b. *Gnathodus mononodosus* sp. nov.—oral view. 68c. *Gnathodus mononodosus* sp. nov.—aboral view. 69a. *Gnathodus commutatus*—lateral view. 69b. *Gnathodus commutatus*—oral view. 70a. *Gnathodus homopunctatus*—lateral view. 70b. *Gnathodus homopunctatus*—oral view. 71a. *Spathognathodus* cf. *cristulus*—lateral view. 71b. *Spathognathodus* cf. *cristulus*—oral view.

Gnathodus girtyi collinsoni Assemblage Zone. 72a. *Gnathodus girtyi collinsoni* subsp. nov.—oral view. 72b. *Gnathodus girtyi collinsoni* subsp. nov.—lateral view. 73a. *Gnathodus girtyi simplex*—oral view. 73b. *Gnathodus girtyi simplex*—lateral view. 74a. *Gnathodus girtyi girtyi*—oral view. 74b. *Gnathodus girtyi girtyi*—lateral view. 75a. *Gnathodus nodosus*—lateral view. 75b. *Gnathodus nodosus*—lateral view. 75c. *Gnathodus nodosus*—aboral view. 76a. *Gnathodus mononodosus* sp. nov.—lateral view. 76b. *Gnathodus mononodosus* sp. nov.—oral view. 76c. *Gnathodus mononodosus* sp. nov.—aboral view. 77a. *Gnathodus bilineatus*—oral view. 77b. *Gnathodus bilineatus*—lateral view. 78. *Prioniodina stipans*—lateral view. 79. *Prioniodina subaequalis*—lateral view. 80. *Neoprioniodus scitulus*—lateral view. 81. *Neoprioniodus tulensis*—lateral view. 82. *Ligonodina levis*—inner lateral view.

first appearance of *Spathognathodus* cf. *robustus* (Branson & Mehl), *S. tridentatus* (E. R. Branson) and *S. anteposicornis* Scott.

REMARKS : This zone occupies nearly all the Upper K Zone in the North Crop and the lower part of the Upper K Zone in the Avon Gorge (Samples K 12–K₂₁ in the Avon Gorge and Samples KL 16–KL 18 on the North Crop). It is correlated with the Upper Cu I and basal Cu II α of West Germany, the lower part of the Upper Hannibal Formation of North America and with part of the Tn_{2c} of Belgium.

On the North Crop a covered shale interval is present between Samples KL 13 and KL 16. In the Avon Gorge Samples K 12–K 17 contain *P. variabilis* gen. et sp. nov. and *S. plumulus* s.s. sp. nov., associated with the *P. inornatus* group. On the North Crop (Samples KL 16–KL 18) *P. variabilis* gen. et sp. nov. and *S. plumulus* s.s. sp. nov. are absent from the zone. *S. isosticha* (Cooper) has not been found in the Avon Gorge, but there is a concealed interval above K 17 and below K₂₁. There are thus two subzones within this assemblage zone. The lower corresponds to Samples K 12–K 17 in the Avon Gorge and occupies the covered interval between KL 13 and KL 16 on the North Crop ; the upper subzone (KL 16–KL 18 of the North Crop) occupies the concealed interval above K 17 and below K₂₁ in the Avon Gorge.

Spathognathodus cf. *robustus*—*Spathognathodus tridentatus* Assemblage Zone

CHARACTERISTIC SPECIES : *S.* cf. *robustus* (Branson & Mehl), *S. elongatus* (Branson & Mehl), *S. tridentatus* (E. R. Branson), *S. crassidentatus* (Branson & Mehl) and *S. anteposicornis* Scott.

LIMITS : The base of this zone is marked by the first occurrence of *Spathognathodus* cf. *robustus* (Branson & Mehl), *S. tridentatus* (E. R. Branson) and *S. anteposicornis* Scott.

The top of the zone is marked by the first occurrence of *Spathognathodus costatus costatus* (E. R. Branson). The final appearance of the *Polygnathus inornatus* group is within the lower part of the zone.

REMARKS : This zone occupies the upper part of the Upper K Zone in the Avon Gorge (Sample K₂₁) and the uppermost K and basal Z Zone on the North Crop (Samples KL 19–ZLA 1). It is correlated with the upper part of the Hannibal Formation of North America, with the Lower Cu II α of Germany and with the Upper Tn_{2c} of Belgium (see also p. 56).

The lower part of this zone (with the *P. inornatus* group) probably occurs in the concealed interval beneath Sample K₂₁ in the Avon Gorge.

Spathognathodus costatus costatus—*Gnathodus delicatus* Assemblage Zone

CHARACTERISTIC SPECIES : In both the Avon Gorge and the North Crop : *S. costatus costatus* (E. R. Branson), *S. costatus sulciferus* (Branson & Mehl), *S.* cf. *cristulus* Youngquist & Miller, *S. cyrius* (Cooper), *S. crassidentatus* (Branson & Mehl), *G. delicatus* Branson & Mehl, *Ligonodina beata* nom. nov., *Hindeodella corpulenta*

Branson & Mehl, *Hindeodella subtilis* Ulrich & Bassler. In the Avon Gorge : *Pseudopolygnathus primus* Branson & Mehl, *Pseudopolygnathus* cf. *dentilineatus* E. R. Branson, *Pseudopolygnathus postinodosus* sp. nov. On the North Crop : *Clydagnathus unicornis* gen. et sp. nov., and *Gnathodus simplicatus* sp. nov.

LIMITS : The base of this assemblage zone is marked by the first occurrence of *S. costatus costatus* (E. R. Branson) and *S.* cf. *crisulus* Youngquist & Miller. The top of the assemblage zone is recognized by the incoming of abundant *Pseudopolygnathus multistriatus* Mehl & Thomas and by the replacement of *G. delicatus* Branson & Mehl by *G. semiglaber* (Bischoff) and *G. antetexanus* Rexroad & Scott.

REMARKS : This zone occupies the uppermost K, the Z₁ and the lower part of the Z₂ Subzones in the Avon Gorge and most of the Z Zone on the North Crop. (Avon Gorge Samples K 18-Z 25 : North Crop Samples ZLA 2-ZLA 28). It is correlated with the uppermost Hannibal, the Lower and Upper Chouteau Formation of North America, with the Middle and Upper Cu II α of Germany, and with the uppermost Tn_{2c} and the Tn_{3a} of Belgium.

This assemblage zone shows some geographical differences. *Spathognathodus costatus costatus* (E. R. Branson) first appears in the North Crop at the base of Sample ZLA 2, some distance within the Z Zone, and is quickly followed by *S. costatus sulciferus* (Branson & Mehl). In the Avon Gorge, on the other hand, these two species are present in the uppermost beds of the K Zone. It is believed that *Pseudopolygnathus primus* Branson & Mehl evolved from *S. costatus sulciferus* Branson & Mehl. In the Avon Gorge at the base of the Z Zone there is a burst of pseudopolygnathids and the genus *Pseudopolygnathus* dominates the early Z Zone fauna. The genus *Pseudopolygnathus* is not present in the Lower Z Zone in the North Crop, its position in the natural conodont assemblages of the Z Zone on the North Crop being represented by other form genera.

As a result, the following three subzones are recognized on the North Crop :

- C. *Clydagnathus unicornis* (Samples ZL 11-ZLA 28).
- B. *Gnathodus simplicatus* (Samples ZLA 15-ZL 10).
- A. *Spathognathodus costatus costatus*-*Spathognathodus costatus sulciferus* (Samples ZLA 2-ZLA 14).

The base of the *Spathognathodus costatus costatus*-*Spathognathodus costatus sulciferus* Assemblage Subzone is marked by the first occurrence of *S. costatus costatus* (E. R. Branson) and *S.* cf. *crisulus* Youngquist & Miller. The subzone is recognized by the presence of the above, together with *S. costatus sulciferus* (Branson & Mehl), *Gnathodus delicatus* Branson & Mehl, and *Apatognathus varians* Branson & Mehl. The *Gnathodus simplicatus* sp. nov. Assemblage Subzone is recognized by the first occurrence of *Gnathodus simplicatus* sp. nov. and the presence of *Gnathodus* sp. B. The top of this assemblage subzone is marked by the final occurrence of *P. communis* Branson & Mehl, *N. barbatus* (Branson & Mehl), *S. costatus sulciferus* (Branson & Mehl) and *A. varians* (Branson & Mehl). The *C. unicornis* gen. et sp. nov. Assemblage Subzone is marked by the paucity of the conodont fauna. What fauna there is, is dominated by the presence of *C. unicornis* gen. et sp. nov., which up to this point has been extremely rare. The top of this subzone is marked by the

disappearance of *S. tridentatus* (E. R. Branson), *Clydagnathus darensis* gen. et sp. nov., *C. unicornis* gen. et sp. nov. and *S. crassidentatus* (Branson & Mehl).

In the Avon Gorge there are two subzones : a lower subzone characterized by the presence of *S. costatus costatus* (E. R. Branson), *S. costatus sulciferus* (Branson & Mehl) and *S. cf. cristulus* Youngquist & Miller, with very few pseudopolygnathids present, (Samples K 18-Z 9) and an upper zone of pseudopolygnathids (Samples Z 10-Z 25). In the subzone of abundant pseudopolygnathids, *Pseudopolygnathus primus* (Branson & Mehl) and *Pseudopolygnathus cf. dentilineatus* are abundant. *Pseudopolygnathus multistriatus* Mehl & Thomas has its lowest stratigraphic occurrence in Sample Z 23.

Polygnathus lacinatus Assemblage Zone

CHARACTERISTIC SPECIES : *Polygnathus lacinatus* s. s. Huddle, *Polygnathus lacinatus asymmetricus* subsp. nov., *Pseudopolygnathus nodomarginatus* (E. R. Branson), *Spathognathodus pulcher* Branson & Mehl and *Pseudopolygnathus multistriatus* Mehl & Thomas. *Gnathodus antetexanus* Rexroad & Scott, is present near the base of the zone in the North Crop and at Farlow.

LIMITS : The lower limit is marked by the incoming of the *P. lacinatus* group and of *Gnathodus semiglaber* (Bischoff). It is also a zone of abundant *Pseudopolygnathus multistriatus* Mehl & Thomas. The upper limit is marked by the incoming of *Pseudopolygnathus cf. longiposticus* (Branson & Mehl).

REMARKS : This zone occupies the uppermost part of the Z sequence in the North Crop and occurs near, but not at the top of, the Z Zone in the Avon Gorge, (North Crop Samples ZLA 29-ZL 19 : Avon Gorge Samples Z 26-Z 32). It is correlated with the unconformity at the base of the Sedalia Formation of North America, with the lowest Cu II β - γ of Germany and with the base of Tn_{3b} of Belgium. The presence of *G. semiglaber* and *P. multistriatus* in this zone indicates its broad equivalence to the Sedalia Formation, but the fact that it also contains abundant *G. delicatus* also implies a similarity to the underlying Upper Chouteau Formation. These two formations are separated by an unconformity in the Mississippi Valley, below which abundant *G. delicatus* occur, but above which this species is absent. It seems probable that beds Z 26-28, in which the two groups of species overlap, are broadly equivalent to the Chouteau-Sedalia unconformity time interval of the Mississippi Valley (see also p. 59).

Polygnathus lacinatus—*Pseudopolygnathus cf. longiposticus*

Assemblage Zone

CHARACTERISTIC SPECIES : *G. semiglaber* (Bischoff), *G. delicatus* Branson & Mehl, *P. cf. longiposticus* (Branson & Mehl), *Polygnathus lacinatus* s.s. Huddle, *Spathognathodus pulcher* Branson & Mehl, *Gnathodus simplicatus* sp. nov. and *Gnathodus avonensis* sp. nov.

LIMITS : The lower limit is marked by the lower limit of abundant *P. cf. longiposticus* (Branson & Mehl). It is also a zone of abundant *Gnathodus*. The upper

limit is marked by the disappearance of *P. cf. longiposticus* (Branson & Mehl) and by the replacement of *G. semiglaber* (Bischoff) by *G. antetexanus* Rexroad & Scott in the Avon Gorge.

REMARKS : This assemblage zone occupies the uppermost part of the Z Zone in the Avon Gorge (samples Z 33–Z 38). It is absent, owing to an unconformity, in the North Crop. It is correlated with the Fern Glen Formation of North America, the Middle Cu II β – γ of Germany, and the Tn_{3b} in Belgium.

Gnathodus antetexanus—*Polygnathus lacinatus* Assemblage Zone

CHARACTERISTIC SPECIES : *Polygnathus lacinatus* s.s. Huddle, *Apatognathus geminus* (Hinde), *Apatognathus scalenus* (Varker), *Apatognathus petilus* Varker, *S. cf. cristulus* Youngquist & Miller and *G. antetexanus* Rexroad and Scott.

LIMITS : The lower limit of the zone is marked by the youngest occurrence of *P. cf. longiposticus* (Branson & Mehl). The lower limit of the genus *Apatognathus* in the Avon Gorge is near the lower limit of the zone. The upper limit of the zone is marked by the oldest stratigraphic occurrence of *Mestognathus beckmanni* Bischoff.

REMARKS : This zone occupies the lower part of the C₁ Subzone in the Avon Gorge (Samples C 1–C 14). It is not present on the North Crop. It is correlated with the lower, middle and lower upper parts of the Burlington Formation of North America, with the upper part of Tn_{3b} and possibly the lowest Tn_{3c} of Belgium and with the Upper Cu II β – γ of Germany.

In this assemblage zone conodonts are sparse. The genus *Pseudopolygnathus* is represented by a considerably smaller number of specimens than in the underlying zone. Specimens of the *P. lacinatus* group, *S. cf. cristulus* Youngquist & Miller and *A. scalenus* (Varker) dominate the fauna. The youngest stratigraphic occurrence of *P. communis communis* Branson & Mehl in the Avon Gorge is within this zone.

Mestognathus beckmanni—*Polygnathus bischoffi* Assemblage Zone

CHARACTERISTIC SPECIES : *Mestognathus beckmanni* Bischoff, *S. cf. cristulus* Youngquist & Miller, *Polygnathus bischoffi* sp. nov., *A. scalenus* Varker, *A. petilus* Varker, and *A. geminus* (Hinde).

LIMITS : The lower limit of the zone is defined by the oldest stratigraphic occurrence of *Mestognathus beckmanni*. The upper limit probably coincides with the zone of maximum abundance of *G. texanus* (Roundy).

REMARKS : This assemblage zone occupies the upper part of the C₁ Subzone in the Avon Gorge (Samples C 15–C 25). It is correlated with part of the Upper Burlington Formation of North America, with the lowest Cu II δ of Germany and with part of the Tn_{3c} of Belgium.

The upper limit of this assemblage zone cannot be defined in the Avon Gorge, because the lower beds of the *Caninia* Dolomite do not contain conodonts.

The conodont fauna obtained from the Upper Avonian C₂, S₁, S₂, and D Zones of the Avon Gorge is sparse in comparison with that obtained from the Lower Avonian.

A gap is present in the conodont record of the lower part of the *Caninia* Dolomites (Samples C 26–C 28). Dr. S. C. Matthews (personal communication) has a small fauna of *anchoralis-bilineatus* interval aspect from an oolitic facies in the Mendips, which represents the lateral equivalent of the *Caninia* Dolomite. This fauna correlates with part of the Cu II δ of Western Europe and with the Keokuk Formation of North America.

***Cavusgnathus unicornis*—*Apatognathus libratus* Assemblage Zone**

CHARACTERISTIC SPECIES : *Apatognathus libratus* Varker, *Cavusgnathus unicornis* Youngquist & Miller, *S. cristulus* Youngquist & Miller, *M. beckmanni* Bischoff, *Gnathodus cuneiformis* Mehl & Thomas, *Cavusgnathus charactus* Rexroad, and *Cavusgnathus cristatus* Branson & Mehl.

LIMITS : The lowest occurrence of the zone in the Avon Gorge coincides with the oldest stratigraphic occurrence of *Cavusgnathus unicornis* Youngquist & Miller, although the true base of the assemblage zone cannot be accurately defined because of the absence of conodont faunas in the *Caninia* Dolomite. One sample (C 39) of the *Caninia* Dolomite has yielded a fauna containing *C. unicornis* Youngquist & Miller and *M. beckmanni* Bischoff. This indicates that at least the upper part of the *Caninia* Dolomite is within this assemblage zone. The upper limit of the assemblage zone coincides with the oldest stratigraphic occurrence of *Taphrognathus varians* Branson & Mehl, which is found in the Upper S₂ Subzone.

REMARKS : This assemblage zone occupies the C₂S₁ Zone and the lower and middle of the S₂ Subzone (Samples C 39–S 44). Together with the overlying *Taphrognathus varians*—*Cavusgnathus*—*Apatognathus* Assemblage Zone, it is equivalent to the middle and upper part of Cu II δ in Europe and to the Warsaw, Salem, and lower part of the St. Louis Formation of North America.

The very small number of conodonts present in this stratigraphic interval precludes a more detailed division, although the presence of *G. cuneiformis* Branson & Mehl at the base of the assemblage zone may provide the basis for future correlation. The overall aspect of the conodont faunas from this and the overlying conodont assemblage zone of the Avonian are similar to those described by Rexroad & Collinson (1963 and 1965) (see p. 61 for detailed discussion).

***Taphrognathus varians*—*Cavusgnathus*—*Apatognathus* Assemblage Zone**

CHARACTERISTIC SPECIES : *T. varians* Branson & Mehl, *C. unicornis* Youngquist & Miller, and *S. cristulus* Youngquist & Miller.

LIMITS : The limits of this assemblage zone coincide with the stratigraphic range of *T. varians* Branson & Mehl as at present known in the Avonian.

REMARKS : This assemblage zone is present in the upper part of the S₂ Subzone of the Avonian (Samples S 45–S 58). It is tentatively correlated with the lower part of the St. Louis Formation of North America. It is equivalent to the uppermost Cu II δ in Germany.

Specimens transitional between *Cavusgnathus* and *Taphrognathus*, which are

identical to those from the St. Louis illustrated by Rexroad & Collinson (1963), have been found in this assemblage zone.

Apatognathus geminus—*Cavusgnathus* Assemblage Zone

CHARACTERISTIC SPECIES : *Cavusgnathus* spp. and *Apatognathus geminus* (Hinde).

LIMITS : The lower limit is marked by the last appearance of *Taphrognathus varians* Branson & Mehl. The upper limit of the zone is marked by the first appearance of *Gnathodus bilineatus* (Roundy).

REMARKS : This assemblage zone occupies the Upper S₂ and the D₁ Subzones (Samples S 59–D 9). No D₁ Subzone conodonts were recovered from the North Crop. The assemblage zone is one of few conodonts, but is characterized by the presence of the genera *Apatognathus* Branson & Mehl and *Cavusgnathus* Harris & Hollingsworth. It is tentatively correlated with the *Apatognathus geminus*–*Cavusgnathus* Assemblage Zone of North America, which is found in the upper part of the St. Louis Formation. This is equivalent to the lowest part of Cu III α in Germany.

Sample D 10 which marks the first appearance of *G. bilineatus* (Roundy) is tentatively taken as the basal sample of D₂ although the D₁–D₂ boundary in the type section is difficult to determine. One anomalous feature of this zone is the occurrence of a fauna from the North of England associated with *Bollandoceras hodderense* (B₁). This would generally be correlated with S₂ of the Avonian (e.g. Thomas & Prentice 1965 : 43). This fauna includes *M. bipluti* Higgins with *G. symmutatus* sp. nov., *G. girtyi simplex* Dunn, *G. commutatus* Branson & Mehl, *G. bilineatus* (Roundy) and *G. homopunctatus* Ziegler.

The subsequent assemblage zones were established from the D₂ and D₃ successions on the North Crop. The few scattered conodonts of this age that were recovered from the Avon Gorge show a general similarity to the North Crop faunas.

Mestognathus beckmanni—*Gnathodus bilineatus* Assemblage Zone

CHARACTERISTIC SPECIES : *Mestognathus beckmanni* Bischoff, *Cavusgnathus unicornis* Youngquist & Miller, *Spathognathodus scitulus* (Hinde), *Apatognathus bladius* sp. nov., *Hibbardella abnormis* Branson & Mehl, *Neoprioniodus montanaensis* (Scott), *Gnathodus girtyi girtyi* Hass, *G. bilineatus* (Roundy), and indeterminate magnilaterellids.

LIMITS : The lower limit of the zone is tentatively taken as the first appearance of *G. bilineatus* (Roundy), but the absence of conodonts in samples of D₁ North Crop strata makes this position provisional. Further collecting will probably reveal an earlier occurrence of this species, which is present in Cu III α of Germany. The top of the zone is marked by the incoming of *G. mononodosus* sp. nov.

REMARKS : This assemblage zone is represented by the lowest 60 ft. of the D₂ Subzone of the North Crop (Samples CYD 1–CYD 6). It is equivalent to part of the Cu III α in Germany, and broadly equivalent to the St. Genevieve Formation of the Mississippi Valley. The zone is no younger than the P_{1b} Subzone of Northern England.

Gnathodus monodosus Assemblage Zone

CHARACTERISTIC SPECIES : *Gnathodus girtyi simplex* Dunn, *G. girtyi girtyi* Hass, *G. monodosus* sp. nov., *G. bilineatus* (Roundy), *G. commutatus* (Branson & Mehl), *G. homopunctatus* Ziegler, and *Spathognathodus cristulus* Youngquist. *Mestognathus neddensis* sp. nov. and *M. bipluti* Higgins are characteristic of this zone in the North Crop.

LIMITS : The lower limit is marked by the first appearance of *G. monodosus* sp. nov. The upper limit is marked by the first appearance of *Gnathodus girtyi collinsoni* subsp. nov. The latter subspecies has not yet been recorded from the Midlothian section, however.

REMARKS : This zone is represented by the highest 10 ft. of the D₂ Subzone and by the lowest 6 ft. of the D₃ Subzone (Samples CYD 7-3D 7) in the North Crop. Our Yoredale samples have yielded no mestognathids. No mestognathids are present in the Fife faunas and Collinson & Druce (in press) failed to recover them from their Irish Viséan fauna. We agree with their suggestion that the genus has an irregular geographic distribution. It is not present in the prolific Upper Mississippi Valley faunas of this age. The top of this zone in the Yoredales is the top of the Simonstone Limestone (P_{1a}). It is equivalent to the Cu III β of Germany and to the late Valmeyrans of the Upper Mississippi Valley.

Gnathodus girtyi collinsoni Assemblage Zone

CHARACTERISTIC SPECIES : *Gnathodus girtyi collinsoni* subsp. nov., *G. girtyi simplex* Dunn, *G. girtyi girtyi* Hass, *G. nodosus* Bischoff, *G. monodosus* sp. nov., *G. bilineatus* (Roundy). *Prioniodina stipans* (Rexroad) and *P. subaequalis* (Higgins) are characteristic of the lower part of this zone in the North Crop and in Dunbar. *Neoprioniodus scitulus* (Branson & Mehl), *N. tulensis* (Pander) and *Ligonodina levis* (Branson & Mehl) are characteristic of the higher part in Scotland.

LIMITS : The lower limit is marked by the first appearance of *G. girtyi collinsoni* subsp. nov. The upper limit is not defined in the present study.

REMARKS : This zone is represented by the uppermost 18 ft. of the D₃ Subzone of the North Crop (Samples 3D 8-3D 23). In the Yoredale section it is represented by samples Y 29-Y 10 comprising the Middle P_{1a}, the Five Yard, the Three Yard and the Underset Limestone (P_{2b}-P_{2c}). The zone is equivalent to the Cu III γ of Germany and broadly equivalent to the Lower Chesterian of the Mississippi Valley. It may be partly equivalent to the Lower Namurian, depending on where the upper boundary is ultimately defined. *G. girtyi turritus* Collinson & Druce is known to extend into the Namurian in Eire (Collinson & Druce in press). It is broadly equivalent to the pre-Middle Glen Dean Chesterian faunas of North America.

The establishment of zonal limits in the upper part of the D succession was difficult. The last appearance of *Mestognathus beckmanni*, *Mestognathus bipluti*, *Gnathodus homopunctatus*, and the first appearance of *Cavusgnathus naviculus*, *Gnathodus nodosus* and *Gnathodus girtyi turritus* were each in turn considered as

possible markers for zonal limits, but the first appearance of *Gnathodus girtyi collinsoni* subsp. nov. was the one in our opinion with the most widespread and meaningful application.

Within a broad depositional basin there is a general similarity between the species of "bar and blade" conodonts in each of the upper zones, but these similarities do not extend to more distant areas, and we have therefore not listed them as characteristic of the zones as a whole.

(d) Intra-Avonian correlation in Britain

(i) Avon Gorge—North Crop (Figs. 49–52).

There is a close overall similarity between the Lower K conodont faunas of both the Avon Gorge and the North Crop (Fig. 14). The lowest beds of both are characterized by the presence of *Spathognathodus plumulus plumulus* sp. et subsp. nov. and *Patrog-nathus variabilis* gen. et sp. nov. The absence in the lowest beds of the North Crop of *Pseudopolygnathus vogesi* sp. nov. which is present in the basal beds of the Avon Gorge, probably implies a slightly older age for the North Crop strata. *Siphonodella*, a most important diagnostic genus for the Carboniferous, and the *Polygnathus inornatus* group first appear at comparable horizons in the North Crop and the Avon Gorge. The last appearance of *Siphonodella* in both sections coincides with the first appearance of *Spathognathodus robustus*, a species whose first appearance overlaps the last appearance of the *Polygnathus inornatus* group.

In the Avon Gorge, *Spathognathodus costatus costatus* first appears just below the traditionally accepted K–Z Zone boundary, whereas in the North Crop, it occurs just above it. The general ranges of all these species are so similar in the two areas, that correlation is relatively straightforward. Details are given on p. 36 in the zonal discussion and in Fig. 14.

In spite of the overall lithological similarity between the Lower Z Zone strata in both areas, there is a lack of any detailed resemblance in their platform conodont faunas. We tentatively interpret this as the result of geographical isolation of certain conodontifers (see p. 36). This probably reflects the influence of palaeogeographical factors, in spite of the fact that other studies have suggested a relatively uniform depositional basin in this area during early Z times.

The incoming of *Polygnathus lacinatus* and of characteristic *Pseudopolygnathus multistriatus* in the higher part of the Z Zone of both areas provides a firm basis for correlation. The absence of *Pseudopolygnathus* cf. *longiposticus* in the North Crop suggests that the higher part of the Z Zone is unrepresented there.

S₂ and C₂S₁ rocks from the North Crop have yielded no conodonts, and Avon Gorge faunas of this general age and also of the D₁ Subzone are also sparse. The presence of *Gnathodus bilineatus* near the base of D₂ in both areas re-establishes the correlation in the higher part of the Avonian. Above this level, conodonts are so rare in the Avon Gorge that no useful comparison can be made with the abundant faunas of the North Crop.

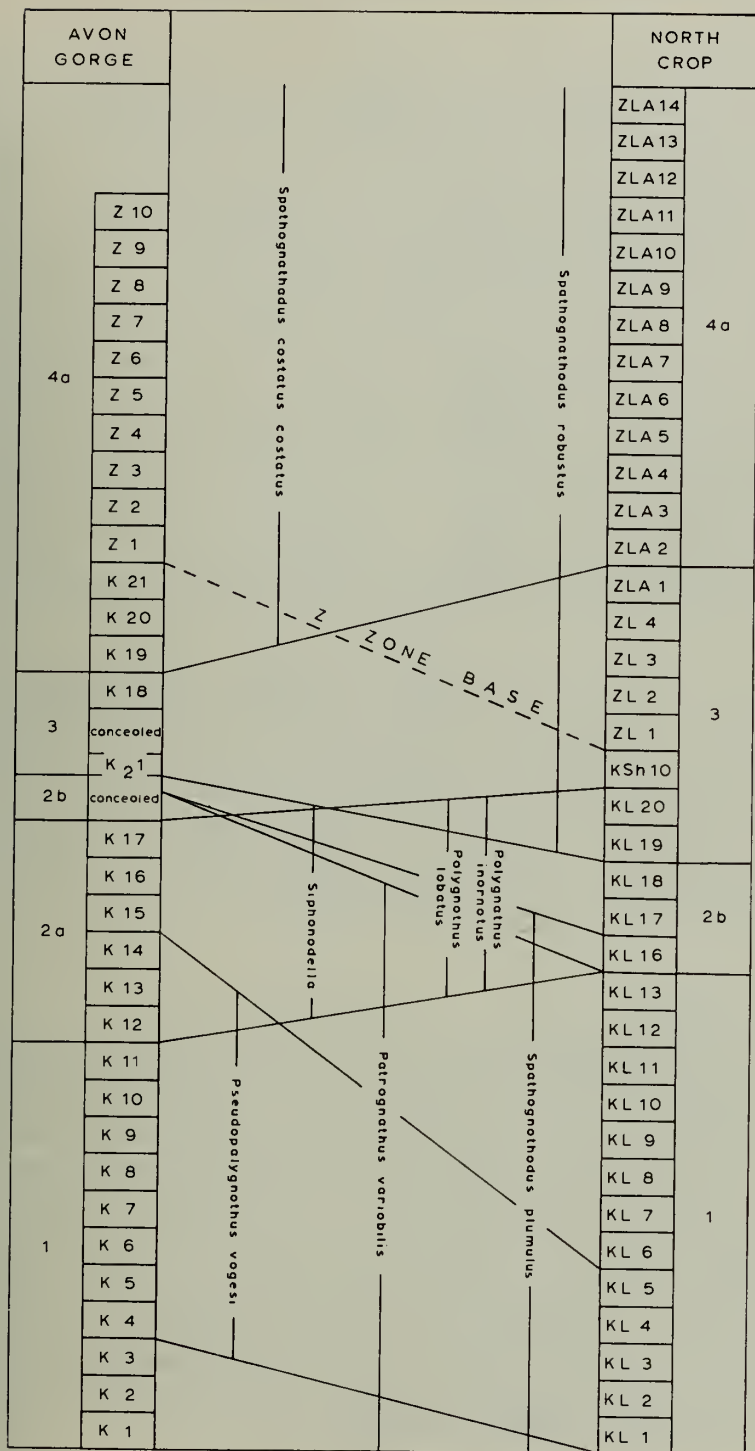


FIG. 14. The correlation of the lower part of the Avonian succession on the North Crop of the South Wales Coalfield and the Avon Gorge, Bristol, showing the relationship between the ranges of species in the two areas.

1 = *P. variabilis*—*S. plumulus* Zone. 2 = *Siphonodella*—*P. inornatus* Zone. (a & b = Lower and Upper Subzones respectively) 3 = *S. cf. robustus*—*S. tridentatus* Zone. 4a = lower part of the *S. costatus*—*G. delicatus* Zone.

(ii) Farlow (Fig. 53).

The K Zone samples from Farlow (FAR 4A-7) yield a fauna broadly similar to that of the lower strata of the Avon Gorge, and the North Crop, although there are some differences. The lowest beds (FAR 4A) are characterized by the presence of both *Patrognathus variabilis* gen. et sp. nov. and *Polygnathus inornatus inornatus*, together with *Clydagnathus gihvernensis* gen. et sp. nov., and *Polygnathus communis*. The first and third of these species occur together in the lowest zone of the Avonian (the *Patrognathus variabilis*-*Spathognathodus plumulus plumulus* Zone) but *Polygnathus inornatus inornatus* is confined to the overlying zone, where it occurs with *P. inornatus rostratus* subsp. nov., which is found in the immediately overlying sample at Farlow (FAR 4), and *P. lobatus* s.l. which is found in the next overlying sample at Farlow (FAR 5). In the Avon Gorge, *P. variabilis* is associated with *Polygnathus inornatus* in this zone. The lowest K Beds of Farlow thus appear younger than those of the North Crop or the Avon Gorge. Furthermore, Sample FAR 5 also contains *Spathognathodus* cf. *robustus*, *S. crassidentatus*, *S. elongatus* and *S. tridentatus*, all of which are characteristic of the *Spathognathodus* cf. *robustus*-*Spathognathodus tridentatus* Zone of the North Crop and Avon Gorge. It therefore appears that the K Zone at Farlow represents a very condensed succession, the overlying beds of the K Zone at Farlow yielding an almost identical fauna to that of Sample FAR 5.

The Z Zone strata at Farlow are marked by the appearance of *Spathognathodus* cf. *crustulus* and *Ligonodina beata* nom. nov. in the lowest beds (ORZ 1) and *Spathognathodus costatus costatus*, and *Clydagnathus darensis* gen. et sp. nov. in the overlying beds (ORZ 2). These species are characteristic of the *Spathognathodus costatus costatus*-*Gnathodus delicatus* Zone, as is *Clydagnathus unicornis* gen. et sp. nov., which occurs in the overlying beds (ORZ 3). A single specimen of *Gnathodus antetexanus* in Sample ORZ A3, represents an anomalous faunal association, since its first appearance in the Avon Gorge is in beds of Z₂ age.

(iii) Yorkshire (Fig. 54).

A reconnaissance sampling programme of the Yoredale succession has yielded abundant and well preserved conodont faunas characteristic of the higher Avonian zones of the South Western Province. Although we have dissolved 7 kilogrammes of the Hawes and Gayle Limestones, the beds have yielded no diagnostic conodonts. The Hardraw Scar and Simonstone Limestones contain *Gnathodus mononodosus* sp. nov. and *G. homopunctatus* and thus fall within the *G. mononodosus* Assemblage Zone. The fauna of the overlying Middle Limestone is marked by the first appearance of *Gnathodus girtyi collinsoni* subsp. nov., and the Five Yard Limestone is characterized by the first appearance of *G. girtyi turritus*. These limestones therefore represent the *G. girtyi collinsoni* Zone. Although Varker (1967) has suggested that species of the genus *Apatognathus* may provide a useful basis for zonation and correlation in the Yoredales, we have found the genus to be rare, rather than common, as he claims, and we do not consider it useful in correlation.

BRITISH GONIATITE ZONES	GERMAN GONIATITE ZONES	CORAL BRACH. ZONES	CONODONT ZONES	YORKSHIRE	AYRSHIRE	MIDLOTHIAN	FIFE	DUNBAR	LITHOLOGICAL GROUPS
E1-2			GNATHODUS GIRTYI COLLINSONI	UPPER LINN LIMESTONE LOWER LINN LIMESTONE INDEX LIMESTONE				BARNES EAST LIMESTONE CHapel POINT LIMESTONE SKATERAW UPPER LIMESTONE	UPPER LIMESTONE GROUP
P ₂				THREE YARD LIMESTONE FIVE YARD LIMESTONE MIDDLE LIMESTONE	HOSIE LIMESTONES DOCKRA LIMESTONE	BILSTON BURN LIMESTONE VEXHIM LIMESTONE	MIDDLE HOSIE LIMESTONE	SKATERAW MIDDLE LIMESTONE SKATERAW LOWER LIMESTONE	LOWER LIMESTONE GROUP
		D ₃	GNATHODUS MONODOSUS	SIMONSTONE LIMESTONE HARDRAW LIMESTONE				LONG CRAIG UPPER LIMESTONE	
P ₁		D ₂			?			HURLET ?	

Fig. 15. Chart to show the correlation of sampled Scottish Carboniferous limestones with the conodont zones established in southern Britain. No precise correlation of limestones within a particular conodont zone is implied.

(iv) Scotland (Figs. 55-58).

Our general descriptions of Scottish faunas represent only a reconnaissance study, our object being to discover whether or not our Avonian zones could be recognized there, rather than to provide any comprehensive solution to the complex problems of correlation of the Carboniferous of that area.

We have suggested a provisional application of our zonal scheme to Scotland (Fig. 15), but have made no precise correlations of individual limestones within particular zones, although we believe this will later prove possible.

Dunbar

In Dunbar the Long Craig Upper Limestone, which was sampled at 6" intervals (DUN 52-71) has a typical *G. mononodosus* Assemblage Zone fauna, which contains a relatively large proportion of mestognathids. The general aspect of this fauna is strongly reminiscent of the uppermost D₂ Subzone of the North Crop. The overlying Skateraw Lower Limestone (DUN 72, 73) yields a typical *G. girtyi collinsoni* Zone fauna although *G. g. collinsoni* subsp. nov. itself is present only in the higher of two limestone samples. This may suggest that the limestone is transitional between this and the underlying zone. The Skateraw Middle Limestone (DUN 74, 82) is barren in its lowest sample, but the overlying sample (DUN 75) yields the first specimens of *G. girtyi turritus*, a subspecies which first appears in the upper beds of the D₃ Subzone on the North Crop. This subspecies continues to be a characteristic member of faunas of higher beds. The Barness East Limestone (DUN 87, 88), although it has yielded only small faunas, is characterized by a very high proportion of cavusgnathids, including both *C. naviculus* and *C. convexus* (Fig. 57).

Midlothian

Although the limestones of the Lower Limestone Group of Midlothian (NGL 1-17, VEX 1, BIL 100-3) have provided no diagnostic species which enable us to correlate them with a precise Avonian conodont zone, the overall aspect of their faunas is strikingly similar to those of the D₃ Subzone of the North Crop. The presence of subspecies of *G. girtyi* and especially the first appearance of *G. g. turritus* in the Vexhim Limestone are useful indications of the general age of these strata (Fig. 56).

The Gilmerton Limestone (GILM 1-7) was collected from the best available section in Midlothian, but this was not the type locality, although we have included it in Fig. 56 in the position of the type Gilmerton Limestone in the Lower Limestone Group succession. It has a fauna of blades, which are more characteristic of higher levels within the D₃ sequence. We therefore suspect that the identification of the limestone at a quarry one mile S.S.E. of Carlops as the Gilmerton Limestone, as given in the Midlothian Coalfield Memoir (1958 : 20), is incorrect.

Fife

The Calciferous Sandstone Measures of Eastern Fife are characterized by relatively few limestone bands in a thick succession of dominantly clastic strata and coals.

Only three samples (ANS 15, 43, 388) have yielded any conodonts, and of these there are few diagnostic species, although the presence of subspecies of *G. girtyi* indicates an overall correlation with the D Zone of the North Crop (Fig. 55).

The Lower Limestone Group has yielded a small fauna from the Hurlet Limestone (HURLET A, C, E) which is characterized by *G. girtyi girtyi* and *G. girtyi simplex*. The Lower Hosie Limestone (HOSIE 1) yields a larger but essentially similar fauna, but the Middle Hosie Limestone (HOSIE 2A-C) has yielded over 1,000 conodonts and is characterized by *G. girtyi collinsoni* subsp. nov., as well as *G. mononodosus* sp. nov. and *G. nodosus*, which suggests a correlation with a high level in the D₃ Subzone of the North Crop.

Ayrshire

The Broadstone Limestone (BRAU 1-8) yielded a very meagre conodont fauna, having an average yield of only one conodont per kilogram of rock. The fauna is characteristic of the *Cavusgnathus unicornis*-*Apatognathus* Zone (Fig. 58).

The Dockra Limestone (BRAU 9 and 10) yields a large and well preserved conodont fauna. *G. girtyi simplex* and *G. girtyi girtyi* each represent almost one third of the total specimens in each sample studied. The presence of *G. girtyi turritus* at the base of the Dockra Limestone shows this to be within the *G.g. collinsoni* Zone.

The Hosie Limestones from Glengarnock (GLEN 1-19) have yielded abundant and well preserved conodont faunas, which include three specimens of *G. g. turritus*, which is indicative of the *G.g. collinsoni* Zone.

The Index Limestone (DR IN 1-GO IN 3) of Ayrshire has yielded faunas which are dominated by *Gnathodus girtyi girtyi*, *G. girtyi simplex* and *G. girtyi collinsoni* subsp. nov., as well as other species characteristic of the *Gnathodus girtyi collinsoni* Zone of the North Crop.

The Lower Linn Spout Limestone (LINL, 1, 3) has yielded only five conodont specimens. These include *G. girtyi girtyi*, *Mestognathus* sp. and *Magnilaterella* sp. which in themselves are not diagnostic.

The Upper Linn Spout (U.LIN 1-7) has a small fauna which includes *G. bilineatus*, *G. mononodosus* sp. nov., *G. nodosus* and *G. commutatus*.

We can make no precise correlation of this formation, but, clearly, the presence of some 300 ft. of underlying strata within the *G. girtyi collinsoni* Zone of Ayrshire implies a relatively young age. We have assigned the Upper Limestone Group to the *Eumorphoceras* Zone on the basis of Currie's (1954 : 535) goniatite faunas from the Index Limestone.

Roxburghshire

The main Algal "Series" of Garwood in Harden Burn yielded abundant and well preserved conodont faunas. These were dominated by the *Polygnathus lacinatus* group and other species including *Cavusgnathus cristatus* and *Taphrognathus varians*. In spite of some differences between this fauna and those of the Avon Gorge, the presence of polygnathids shows the Roxburghshire faunas to be equivalent to the early C Beds of the Avon Gorge. This accords well with the tentative C₁ age assigned to these beds by Garwood (1931).

Summary

Our overall Scottish correlations show a very close similarity to those proposed by Currie (1954, Table 1) on the basis of her goniatite studies. The only difference involves the first appearance of *G. girtyi collinsoni* subsp. nov. in the Middle Hosié Limestone of Fife.

On the basis of this we have proposed the tentative correlation shown in Fig. 15, but it seems probable that the absence of this subspecies from underlying strata is the result of the relatively poor yields of the Lower Hosié (29 individual conodonts) and Hurlét Limestones (15 conodonts).

This diagnostic subspecies is represented by less than 3% of the total fauna of each of the two overlying Middle Hosié samples, each of which comprises more than 400 identifiable conodonts.

(e) Correlation of the Avonian with Europe and North America

The purpose of this section is to discuss the value of conodonts in the correlation of the British type Avonian section with type sections in North America and Western Europe. The sections in the Mississippi Valley, the conodont faunas of which were described by Collinson, Scott & Rexroad (1962), are taken as standard sections for North America, and the West German Lower Carboniferous sections, the conodont faunas of which were described by Bischoff (1957) and Voges (1959), are taken as standard sections for Western Europe. We have also made provisional correlations with the Franco-Belgian Tournaisian Viséan succession, basing our comparisons on the faunas reported, but not described, by Conil, Lys and Mauvier (1964).

The general results of this correlation are most gratifying. We have been able to suggest the relative equivalence of most of the various divisions of the North American, German, French, Belgian and British successions with a sufficient degree of confidence and precision to provide a satisfactory overall stratigraphic control. In those cases where our correlation is more tentative, we have discussed the limits of uncertainty, and these are seldom great. We have had the great advantage of working in virtually continuous Avonian rock sections, and some of the present anomalies between our faunal successions and those of other areas, such as Germany, and, to a lesser extent, the Mississippi Valley, probably lie in the scattered outcrops on which the latter are based. More information is needed from all areas before the present faunal similarities and differences can be fully interpreted.

(i) North America and West Germany

The K and Z Zones of the Avonian.

The K and Z Zones of the Avonian are, in many respects, the most difficult part of the succession to correlate with other areas, largely because of the absence from them of some zonal species, and the presence of new genera and species which are, at present, not known with certainty from other areas.

An important element of the K Zone fauna is the group of new species, which are confined to that zone; these include *Patrognathus variabilis* gen. et sp. nov., *Clyda-*

gnathus gen. nov. and *Spathognathodus plumulus plumulus* sp. nov. Although these species are new, they show some resemblances to specimens described from other areas.

Klapper & Glenister (1966) have described faunas from the Canning Basin of Western Australia. Their “? *Scaphignathus velifera*” is, according to Dr. Klapper (personal communication), probably congeneric with *Clydagnathus*, having a large basal cavity, which removes it from *Scaphignathus*. This species occurs in two samples. In one of these, it is not associated with other conodonts, and lies stratigraphically about 150 ft. below *Spathognathodus aculeatus*. In the other, it occurs with that species and with *Palmatolepis glabra* subsp. indet. It is clearly, therefore, of Upper Devonian age in this area. This does not necessarily imply an Upper Devonian age for the K Zone of the Avonian, however. The resemblance of the Australian specimens to those from the K Zone is not exact, and they may represent distinct species. The association of the Australian specimens with *S. aculeatus* implies an age within the *costatus* Zone and the Tn_{1a} of Belgium, but the absence of *S. aculeatus* in the Avonian K Zone conodont faunas suggests that they are of younger age.

The presence of *Spathognathodus costatus* in the K Zone of the Avonian could imply an Upper Devonian age, but *S. costatus*, as we have now defined it, differs from *S. costatus* of German authors. The relative position of other Avonian genera makes a Carboniferous age even more probable. Our *S. costatus* is confined to beds in the Avonian lying above both *Siphonodella* and our single specimen of *Elictognathus*. Furthermore, the gnathodids, although they first occur 150 ft. above the position of *S. costatus* in the Avon Gorge, are advanced species which are of undoubted Carboniferous age in other areas. The earlier species of *Gnathodus* (*G. kockeli* etc.) are not represented in the Avonian faunas.

Bouckaert & Ziegler (1965) have described a Fammenian conodont fauna from Belgium, in which are found five specimens of *Scaphignathus veliferus* (1965, Pl. 5, figs. 5-7) in a sample from the Montfort section at Esneux. These specimens probably represent the genus *Clydagnathus*, although they do not appear conspecific with forms from the K Zone.

The genus *Palmatolepis* is characteristic of the Upper Devonian but Bischoff (1957) and Voges (1959) have reported *Palmatolepis* in the basal Cu I beds of West Germany. In North America, in the Mississippi Valley, *Palmatolepis* is abundant in the Saverton Shale, common to rare in the Louisiana Limestone and occurs rarely in the basal beds of the Hannibal. Collinson (1961) stated that “the occurrence of *Palmatolepis glabra* and *Palmatolepis gracilis* in the European Lower Carboniferous, as well as in the Mississippi Valley Hannibal Formation, may represent stratigraphic admixture, but it seems more likely that they are indigenous”. Specimens of the vast majority of Upper Devonian faunas yield abundant *Palmatolepis*, and the absence of palmatolepids in the Avon Gorge provides some negative evidence in support of the assignment of the lowermost strata to the Carboniferous.

Fewer than 2% (Klapper & Furnish, 1962 : Ziegler 1962, table 7 : Bouckaert & Ziegler 1965, Chart 9) of the Upper Devonian faunas described lack *Palmatolepis*, and

the genus is present in Devonian faunas in southwestern England. We stress that these are negative data, however; indeed, it seems possible that a few Lower Carboniferous faunules may contain indigenous palmatolepids.

It is possible that our Lower K faunas are close to the fauna briefly described by Bouckaert & Ziegler (1965, Chart 9, p. 25) from the section at Huy 2 in Belgium. The highest part of this section (19) contains a new genus (not described, illustrated, or mentioned in the text) together with *S. aculeatus* E. R. Branson and *Pseudopolygnathus dentilineatus* E. R. Branson. The first of these two species may represent *S. plumulus*. Bouckaert & Ziegler also record from the same sample (1965 : 17), a single specimen of a form "which seems to represent a new trend evolved from *Spathognathodus costatus*" (Pl. 4, fig. 12 and p. 27 : *Pseudopolygnathus* sp.). This is close to our *Pseudopolygnathus vogesi* sp. nov. A Lower Tournaisian age for this part of the Belgian section has been suggested by Conil (1964) on the basis of the foraminifera, and Streel (1966) states that the spores indicate a Devonian age.

Klapper & Sandberg (1967 : B 52) have found the genus *Patrognathus* in a very thin interval of strata in Wyoming (the Windy Gap Formation). It is associated with *Siphonodella sulcata*, a species that was also recovered by these authors from the upper part of the *G. kockeli*-*P. dentilineatus* conodont zone in Germany (Voges 1959, text-fig. 1, Samples 3 and 4).

An undescribed conodont fauna from the Lower Pilton Beds contains *Spathognathodus plumulus* sp. nov., *Pseudopolygnathus vogesi* sp. nov. and representatives of the genus *Clydagnathus* (J. W. Williams, personal communication). The Lower Pilton Beds are considered to be of *Wocklumeria* age (Goldring 1955). However, no specimens of the genus *Patrognathus* have as yet been found in the Lower Pilton Beds. Thus the Lower Limestone Shale appears to be younger than the Lower Pilton Beds. The conodont fauna of the Lower Pilton Beds is unlike the fauna from the *Wocklumeria* to VI Zone described by Ziegler (1962). It is closer to the fauna described by Bouckaert & Ziegler (1965), from the uppermost Fammenian at Huy.

All the evidence points to the conclusion that a gap in the conodont sequence is present in the type section of the Devonian-Carboniferous boundary in the Hönnetal railway cutting. The Huy section of Fammenian age is younger than the type to VI strata at Hönnetal, but on goniatite and spore evidence it is still Devonian. The base of the Lower Limestone Shale is younger than the Huy section (on the basis of the absence of the genus *Patrognathus* in the Huy section), but is older than the base of the Tournaisian in the Hönnetal railway cutting.

Thirty feet above the base of the K section in the North Crop a single specimen of *Elictoagnathus* has been found. *Elictoagnathus* makes its first appearance in North America at the base of the *Siphonodella sulcata* Assemblage Zone which is near the base of the Hannibal Formation, and is correlated with the middle part of the Lower Carboniferous Cu I Zone of Western Europe (Collinson, Scott & Rexroad 1962).

Associated with *Elictoagnathus* in the *Pseudopolygnathus vogesi*-*Clydagnathus* Assemblage Subzone of the Avonian is *Pseudopolygnathus vogesi* sp. nov. This species is characteristic of the lower part of the Lower Carboniferous Cu I Zone of

Western Europe (Voges 1959). Collinson, Scott & Rexroad (1962) noted that the first appearance of the genus *Pseudopolygnathus* in the Mississippi Valley was at the base of their *Gnathodus* n. sp. B.-*Gnathodus kockeli* Assemblage Zone, which is confined to the Glen Park and the basal Hannibal Formations and is correlated with the lowermost part of the Lower Carboniferous Cu I Zone of Western Europe.

The upper part of the *Pseudopolygnathus vogesi*-*Clydagnathus* Assemblage Subzone has specimens of *P. inornatus* which Ziegler (1962), who referred to them as *Polygnathus nodomarginatus*, found in the Middle and Upper *Spathognathus costatus* Zones, as well as in the *G. kockeli*-*P. dentilineatus* Zone. Dr. C. W. Collinson (personal communication) has found similar specimens in the Mississippi Valley, where they appear to be forerunners of *Siphonodella sulcata*. These are found in abundance, and are associated with *Gnathodus kockeli* in the base of the Hannibal Formation at several localities (just below the lowermost *Siphonodella* Zone).

The conodont fauna of the K and basal Z Zones of the Avonian is also difficult to correlate precisely with the American and West German successions, because of the rarity of the genus *Siphonodella* in the K Zone and its absence in the Z Zone. This genus is one of the most useful of all guide fossils in other areas, where individual species are distinctive, short ranging, and have a wide geographical distribution (Collinson, Scott & Rexroad 1962, Chart 2). In North America and West Germany ranges of individual species have been used to define the boundaries of conodont assemblage zones.

In the Avonian, the genus *Siphonodella* is confined to the *Siphonodella*-*Polygnathus inornatus* Assemblage Zone. Specimens from the Avon Gorge, although fractured, have rostral ridges and are more advanced in development than *Siphonodella sulcata*, the earliest known species in North America, where it occurs near, but not at, the base of the Hannibal Formation. Specimens from the North Crop are identified as *Siphonodella isosticha*. This species in North America ranges from the base of the Upper Hannibal Formation to the top of the Upper Chouteau Formation. Thus the base of our *Siphonodella*-*Polygnathus inornatus* Assemblage Zone cannot be older than the base of the upper part of the Hannibal Formation, which is included in the lower part of the *Siphonodella quadruplicata*-*Siphonodella crenulata* Assemblage Zone of the Mississippi Valley.

Correlation of the base of this zone with our *Siphonodella*-*Polygnathus inornatus* Assemblage Zone, would make it broadly equivalent to the lower part of the Cu II α Zone of the European Lower Carboniferous. This is supported, to some extent, by a consideration of the ranges of gnathodid species, which provide a possible correlation for the higher part of the Avonian section.

Klapper (1966) has described a fauna from the Lodgepole Limestone of Montana and Wyoming, which is referable to the Lower *Siphonodella crenulata* Zone (Cu II α) of Germany and from the Mississippian part of the Dark Shale Unit, which is referable to the *Siphonodella*-*P. triangulus triangulus* Zone (Cu I). These faunas are in part similar to the Upper K Zone fauna of the Avonian.

The conodont fauna of the *Spathognathodus robustus*-*Spathognathodus tridentatus*

Assemblage Zone is similar to that described by Branson & Mehl (1934A) from the Bushberg Sandstone of Missouri, while the fauna of the basal *Spathognathodus costatus sulciferus*-*Gnathodus delicatus* Assemblage Zone is similar to that of the Hannibal Formation of Missouri described by E. R. Branson (1934).

Our faunas from the K and Z Zones seem to agree closely with those described by Branson & Mehl (1934A) from the Bushberg, E. R. Branson (1934) from the Hannibal, and Cooper (1939) from the pre-Welden Shale Formations. This suggests that the biostratigraphic zones set up by Collinson, Scott & Rexroad (1962) may not be fully representative of the conodont faunas of the lowermost Lower Carboniferous of the whole of North America, as opposed to the Illinois Basin. Further work on Missouri and Oklahoma sections would probably prove useful in correlation between North America and the South West Province of Great Britain.

Gnathodus delicatus makes its first appearance in the Avonian 34 ft. (Sample ZLA 6 North Crop) from the top of the *Spathognathodus costatus costatus*-*Gnathodus delicatus* Assemblage Zone. In North America this species first appears at the base of the Chouteau Formation, in the top of the *Siphonodella quadruplicata*-*Siphonodella crenulata* Assemblage Zone, but little is known about the distribution of Upper Hannibal gnathodids, and it is therefore possible that *Gnathodus delicatus* may appear lower in the section. The top of the Hannibal Formation is the zone of few gnathodids of Collinson, Scott & Rexroad (1962). A similar zone of few gnathodids is also present in Germany. Branson & Mehl (1938A : 136) remarked that the Chouteau conodont assemblage is characterized by the introduction of *Gnathodus*. The base of the Chouteau Formation also corresponds to the oldest stratigraphical occurrence of the upper zone of *Gnathodus* shown by Collinson, Scott & Rexroad (1962, Chart 3).

The earliest occurrence of *Gnathodus delicatus* in the Avon Gorge, which is somewhat higher (base Sample Z 29) in the section than the earliest occurrence on the North Crop, is represented by relatively large numbers of specimens, in contrast to the few specimens found in its first occurrence on the North Crop. The earliest occurrence of *Gnathodus delicatus* on the North Crop may be correlated to the *Siphonodella quadruplicata*-*Siphonodella crenulata* Assemblage Zone occurrence of North America, which lies within the Zone of few gnathodids, whereas the Avon Gorge first occurrence may be correlated with the abundant occurrence of *Gnathodus delicatus* in North America, near the upper limit of the *Siphonodella isosticha*-*Siphonodella cooperi* Assemblage Zone, which occupies the upper part of the Chouteau Formation and is correlated with the upper part of the European Lower Carboniferous Cu II α Zone.

Rexroad & Scott (1964) described the conodont faunas from the *Siphonodella isosticha*-*Siphonodella cooperi*, *Gnathodus semiglaber*-*Pseudopolygnathus multistriatus*, *Bactrognathus*-*Polygnathus communis* and *Bactrognathus*-*Taphrognathus* Assemblage Zones, when they described the conodont fauna of the Rockford Limestone and New Providence Shale. They noted (Table 2 : 15) that *Gnathodus delicatus* was most abundant in the *Siphonodella isosticha*-*Siphonodella cooperi* Assemblage Zone, *Gnathodus semiglaber* most abundant in the overlying *Gnathodus semiglaber*-*Pseudopolygnathus multistriatus* Assemblage Zone and *Gnathodus antetexanus* most

abundant in the overlying *Bactrognathus*-*Polygnathus communis* Assemblage Zone.

In the Avonian of the Avon Gorge a similar change in the gnathodid fauna is seen. *Gnathodus delicatus* occurs near the base of the Z_2 Subzone, *Gnathodus semiglaber* is present in the upper part of Z_2 and *Gnathodus antetexanus* first appears in the upper part of Z_2 and ranges into the lower part of C_1 (Fig. 11).

The occurrence of gnathodids in Germany provides conflicting data for comparison. Ziegler (1960, 1963) has described gnathodids identical to those of the middle *Polygnathus lacinatus* Zone of the Avonian (Samples Z 28-Z 30). One of his faunules of *anchoralis* age (1960) also contained *Siphonodella* and *Mestognathus*, but the other yielded no representatives of *Siphonodella*. The *anchoralis* fauna of Germany, as at present understood, contains the simultaneous first appearance of several species of *Gnathodus*, which appear at different horizons in the Lower Carboniferous of Britain and North America. We interpret this as partly the result of Bischoff & Voges' limited stratigraphic sections and partly the result of the more recent taxonomic refinements, which would now require the revision of the earlier specific nomenclature of these authors.

Specimens referable to *G. semiglaber*, *G. typicus*, *G. antetexanus* and *G. girtyi* all first appear at the base of the *anchoralis* Zone. It appears that the *anchoralis* Zone as presently defined in Germany occupies a greater period of time than hitherto thought and that the Cu II β - γ with which it is generally equated could include the time interval Upper Z_2 -Upper C_2 in the Avonian and at least from the top of the Chouteau Formation to the top of the Burlington Formation in North America.

If the first appearance of species is used as the basis of correlation, the oldest occurrence of *Gnathodus delicatus* in the Avonian is in the *Spathognathodus costatus costatus*-*Gnathodus delicatus* Zone. In North America it first occurs in the *Siphonodella isosticha*-*S. cooperi* Zone, which might thus be interpreted as being equivalent to the Avonian Zone. This would make it equivalent to the Upper Chouteau, and to the upper part of Cu II α of the German succession (Figs. 12, 16). Collinson, Rexroad & Scott (1962) noted that the top of the *Siphonodella isosticha*-*Siphonodella cooperi* Assemblage Zone was marked by a major unconformity in the Mississippi Valley and was a cut-off horizon for *Gnathodus delicatus*. This is one possible correlation, but the rarity of siphonodellids in the Avonian makes any such correlation based on "first appearances" of species tenuous, and other aspects of the fauna suggest a somewhat younger (Chouteau) age for the Avonian Zone.

The *Siphonodella*-*Polygnathus inornatus* Zone is also characterized by the presence of *Polygnathus inornatus* s.l. and *Siphonodella isosticha*, both of which are characteristic species of the *Siphonodella isosticha*-*S. cooperi* Zone of the Mississippi Valley (Collinson, Scott & Rexroad 1962 : 21). Correlation of these two zones would thus appear an alternative valid solution to the problem, the general absence of earlier transitional siphonodellids in the Avonian being interpreted as a result of geographic faunal variation, either in the absence of whatever conodont-bearing group they represented, or, more probably, their "local" functional replacement by broadly homologous polygnathids (Fig. 16).

Such a possible correlation is supported by the fact that in the Bonaparte Gulf of

MISSISSIPPI VALLEY SCHEME A	AG 100 Conodont Ranges	GENERALISED AVON GORGE NORTH CROP	CONODONT RANGES	MISSISSIPPI VALLEY SCHEME B	BONAPARTE GULF, AUSTRALIA SUCCESSION
Bactrognathus-Polygnathus communis Zone	C1	Polygnathus laciniatus - pseudopolygnathus cf. prolongiposticus Zone	C1	Burlington	Pseudopolygnathus nadamarginatus
Gnathodus semigaber - Pseudopolygnathus multistriatus Zone	Z	polygnathus laciniatus Zone	Z	Fern Glen	Septimus Limestone
Siphonadella isosticha - Siphonadella cooperi Zone	Z	Spathognathodus costatus costatus - Gnathodus delicatus Zone	Z		Spathognathodus costatus sulciferus
Siphonadella quadruplicata - Siphonadella crenulata Zone	K	Spathognathodus cf. S. robustus - S. tridentatus Zone	K		Spathognathodus robustus
Siphonadella duplicata Zone	K	Siphonadella - Polygnathus innata Zone	K	Upper Chouteau	Siphonadella isosticha Siphonadella obsolleta Polygnathus innatus
Siphonadella sulcata Zone	K	Patrognathus varriabilis - Spathognathodus plumulus plumulus Zone	K	Lower Chouteau Upper Hannibal Middle Hannibal	Siphonadella crenulata Siphonadella sulcata
				Lower Hannibal	Pseudopolygnathus vogesi - Clydagnathus Zone

FIG. 16. Chart to show two possible correlations between the Avon Gorge—North Crop Lower Carboniferous succession and that of the Mississippi Valley. Scheme A is based upon the ranges of species of *Gnathodus* and Scheme B based chiefly on the ranges of species of *Siphonadella*. The Bonaparte Gulf succession of Australia is also shown.

Australia one of us (*in* Jones & Druce 1966) has recently discovered a series of abundant conodont faunas extending through some 3,000 ft. of Lower Carboniferous strata. There is a striking resemblance between the Australian and the Avonian conodont successions, and although *Siphonodella* is abundant in the Australian faunas, it does not extend up as high as the *Spathognathodus costatus* group (Fig. 16). This could mean that all the *Siphonodella* zones of the Mississippi Valley lie below the first occurrence of *S. costatus* in the Avonian, and would therefore be of K age.

The other implication of such a correlation would be that the North American and the German successions are more incomplete than has formerly been supposed, for it would be difficult to find any North American equivalent of the two overlying Avonian assemblage zones, if the correlation of the Avonian *Polygnathus lacinatus* Zone and the Mississippian *Gnathodus semiglaber*-*Pseudopolygnathus multistriatus* Zone (which seems to us to be very well established, p. 57) is accepted. This would suggest that the unconformity known to exist beneath the Sedalia Formation of the Mississippi Valley, is of greater magnitude than is generally assumed.

There may not be such a break in the Oklahoma or parts of the Missouri successions (Cooper 1939; Branson & Mehl 1934A: 265). The Rockford Limestone fauna (Rexroad & Scott 1964) reveals an apparent transition in northern Indiana from the *Siphonodella isosticha*-*S. cooperi* Zone into the *Gnathodus semiglaber*-*Pseudopolygnathus multistriatus* Zone, however, and represents an anomaly if the present correlation is accepted, although most of the sections come from cores. There is, however, an unconformity in southern Indiana between the Rockford and the overlying New Providence Shale. Even in areas of apparent transition of the two assemblage zones within the Rockford Limestone, the faunal transition is abrupt (Rexroad & Scott 1964, Table 1). Rexroad & Scott (1964: 16-17) have written "Although a number of species are common . . . this break between the Kinderhook and Osage Series is unusually well marked. The faunal break is sharp, but a number of species confined to the lower zone gradually decrease in number upward. Thus an unconformity within the Rockford at the Kinderhook-Osage boundary is not necessarily indicated. At the type section near Rockford (locality 10) the formation is exposed only in the bed of the East Fork of White River, and even at low water the evidence relating to a possible unconformity cannot be interpreted."

It may also be that the overlap of the *Siphonodella* and *anchoralis* faunas in Germany implies a stratigraphic break between them, in which case part of the Upper Cu II α and Lower Cu II β could be unrepresented. One of the major problems concerning the *anchoralis* fauna is its patchy geographic distribution (p. 65). It is possible that its limited distribution in North America (it is recorded from the Pierson Formation of Missouri and the "Sedalia" of Illinois, above the unconformity) may mean that in places it is represented by the unconformity which we have postulated.

This alternative correlation has stressed the inadequate numbers of siphonodellids in British Lower Carboniferous faunas, and its weakest point is the lack of a more detailed series of species of this genus in the Avonian. The first provisional correla-

lation, in which the ranges of gnathodid species were compared, is also limited by a comparable, tantalizing "zone of few gnathodids" in the Middle and Upper Hannibal of North America, and if, as we believe, both correlations are equally reasonable, they are also equally vulnerable, because of a comparable lack of detailed phylogenetic development in Britain and the United States.

The present available data are insufficient to allow us to make a final choice between the two alternative correlations; although we have shown the second on our main correlation table (Fig. 12), we have summarized the evidence for both on Fig. 16). The total stratigraphic differences involved between them are not great, and it is perhaps a paradoxically satisfying aspect of the precision which we believe conodonts offer, that we should be dissatisfied with an uncertainty of some 80 ft. in such a transatlantic correlation.

A new conodont fauna associated with the goniatites *Protocanites* and *Muensteroceras* from the Berwick Formation of Australia (Dr H. T. B. Jenkins, personal communication) contains a fauna which is similar to the Z Zone fauna of the Avonian in many respects. The pseudopolygnathids are identical to Z₁ and Lower Z₂ specimens. Associated with the pseudopolygnathids are many gnathodids, most of which are new species, although a few are similar to *G. punctatus*, a species characteristic of the upper part of Z₂. Two specimens of *Bactrognathus* also occur in the Australian fauna, suggesting that *Bactrognathus* is older than has hitherto been thought likely.

The fauna of Samples Z 31 to Z 38 with *Gnathodus semiglaber* and *Pseudopolygnathus multistriatus* is similar to that of the *Gnathodus semiglaber*-*Pseudopolygnathus multistriatus* Assemblage Zone of the Mississippi Valley. This Assemblage Zone coincides with the "Sedalia" Formation of the Mississippi Valley and has been correlated with the lowermost part of the Cu II β Zone of Western Europe. Dr W. Ziegler (personal communication) believes that the gnathodid fauna of Samples Z 34-Z 38 is identical to that found in Western Europe in beds equivalent to the *Siphonodella crenulata* Zone (Voges 1959) and thus of Cu II α age.

C Zone.

In the upper part of the Z Zone and in the lower part of the *Laminosa* Dolomite, *Gnathodus antetexanus* has been found, associated with *Pseudopolygnathus* cf. *triangulus triangulus*, *Polygnathus communis* and *Polygnathus lacinatus*. The lower limit of the *Bactrognathus*-*Polygnathus communis* Assemblage Zone in the Mississippi Valley coincides with the earliest abundance of *Gnathodus antetexanus*, and the upper with the youngest stratigraphical occurrence of *Polygnathus communis*. In the Avonian of the Avon Gorge, the youngest stratigraphical occurrence of *Polygnathus communis* is in the middle of the *Laminosa* Dolomite (the base of Sample C 10). The *Bactrognathus*-*Polygnathus communis* Assemblage Zone is characterized by the presence of *Polygnathus communis*, *Pseudopolygnathus multistriatus*, *Pseudopolygnathus triangulus pinnatus* and by being the zone of abundant *Gnathodus antetexanus*. Samples Z 38-C 9 are correlated with this Assemblage Zone. In North America, the zone extends from the base of the Fern Glen Formation to the top of

the Middle Burlington Formation. In Western Europe it ranges from upper Cu II β into lower Cu II γ .

In West Germany Bischoff (1957) recorded the first appearance of *Mestognathus beckmanni* at the base of Cu III α , but Voges (1959) found a single specimen near the base of Cu II β/γ . Kronberg, Pilger, Scherp and Ziegler (1960) also found *Mestognathus beckmanni* in beds of Cu II β/γ age. Meischner (1962) in his chart of stratigraphic ranges (p. 31, fig. 10) showed the stratigraphic range of *Mestognathus beckmanni* as commencing at the base of Cu II β/γ . The lowest occurrence of *M. beckmanni* in the Avonian is in the upper part of the *Laminosa* Dolomite (the base of Sample C 15). Thus the upper part of the *Laminosa* Dolomite appears to be of Cu II β/γ age.

In North America the base of the *Bactrognathus-Taphrognathus* Assemblage Zone is marked by the highest occurrence of *Polygnathus communis*, and the top by the lowest abundant occurrence of *Gnathodus texanus*, which makes its first appearance near the top of the zone. The youngest stratigraphic occurrence of *Polygnathus communis* in the Avonian is in the middle of the *Laminosa* Dolomite. It is considered that the middle of the *Laminosa* Dolomite, above the youngest occurrence of *Polygnathus communis* (base Sample C 10), corresponds to the base of the *Bactrognathus-Taphrognathus* Assemblage Zone of North America. In North America this zone is confined to the upper part of the Burlington Formation and is correlated by Collinson, Scott & Rexroad (1962) with the upper part of the European Cu II β/γ Zone. Since *Mestognathus* has not been recorded from North America, our intermediate faunas provide important confirmation of this correlation.

The *Caninia* Oolite in the Avon Gorge is characterized by the presence of two species, *Polygnathus bischoffi* sp. nov. and *Mestognathus beckmanni*. In Western Europe the youngest stratigraphic occurrence of *Polygnathus bischoffi* sp. nov. is at the top of Cu II β/γ . *Gnathodus texanus* s.s. occurs with *Mestognathus beckmanni* and *Polygnathus bischoffi* sp. nov. in the *Caninia* Oolite of Fall Bay, Gower. Since the youngest occurrence of *Gnathodus texanus* s.s. in North America is near the top of the *Bactrognathus-Taphrognathus* Assemblage Zone, the upper part of the *Laminosa* Dolomite and the *Caninia* Oolite are correlated with the *Taphrognathus-Bactrognathus* Assemblage Zone and with the upper part of the European Cu II β/γ Zones.

A conodont fauna from Askeaton, Eire, contains specimens of *G. texanus*, *P. triangulus pinnatus* and *G. girtyi*. The specimens of *G. girtyi* are identical to those illustrated by Hass (1953) and clearly have developed from *G. texanus*. The Askeaton fauna is therefore younger than the *Caninia* Oolite fauna and is best correlated with the *Caninia* Dolomite.

S and D Zones.

The *Cavusgnathus unicornis-Apatognathus libratus* and the *Taphrognathus varians-Cavusgnathus-Apatognathus* Zones of the Avonian cannot be precisely correlated with the American assemblage zones. Although they have elements in common with both the *Taphrognathus varians-Apatognathus* and the *Apatognathus? geminus-Cavusgnathus* Assemblage Zones of the Mississippi Valley, there are also important

differences between the two faunal successions. The *Taphrognathus varians*-*Apatognathus* Assemblage Zone includes the Warsaw, Salem and the lower part of the St. Louis Formations, and it is probably equivalent to the upper part of the Cu II δ Zone of Western Europe. The limits of this assemblage zone were defined by Collinson, Scott & Rexroad (1962) as follows: "The lower limit is marked by the lowermost occurrence of *Apatognathus?* in the Valmeyeran Series plus the highest occurrence of common *Taphrognathus varians*. The upper limit is distinguished by the lowermost occurrence of *Cavusgnathus* and the youngest occurrence of *Taphrognathus* as well as by the lower limit of the upper zone of abundant *Apatognathus*".

The lowest stratigraphic occurrence in the Avonian of specimens identical to the apatognathids illustrated by Rexroad & Collinson (1963) is near the base of C₁. *Taphrognathus* does not appear in the Avonian until the upper part of the S Zone, well above the first appearance of *Cavusgnathus*. Specimens transitional between *Cavusgnathus* and *Taphrognathus*, identical to those illustrated by Rexroad and Collinson from the boundary between the lower and upper St. Louis Formation, are found in Samples S 49 to S 58 of the Avonian. *Cavusgnathus* first appears in the Avonian in the middle of the *Caninia* Dolomite, well above the first appearance of *Apatognathus*, and well below the first appearance of *Taphrognathus*. In North America, however, the first appearance of *Cavusgnathus* is above the first appearance of *Taphrognathus* and *Apatognathus*.

In the Scottish conodont faunas, *Taphrognathus varians* occurs with *Polygnathus lacinatus*, a species which in the Avonian is common in the upper part of Z₂ and in the C Zone. Thus it would appear that the lowest occurrence of *Taphrognathus* in Britain may be considerably lower than that noted from the Avonian of the South West Province and it would then correspond more closely with the North American occurrence.

The *Apatognathus geminus*-*Cavusgnathus* Assemblage Zone (Upper S₂-D₁ of the Avon Gorge) is equivalent to the upper part of the St. Louis Formation of the Mississippi Valley and to the basal Cu III α of Germany.

In Germany, *Mestognathus beckmanni* ranges from the base of Cu II β/γ (and may extend into Cu II α) to the middle of Cu III γ (Bischoff 1957) although Meischner (1962) gives the upper limit as Middle Cu III β . *Gnathodus bilineatus* is present in the Cu III and E Zones of Germany and Britain (Collinson & Druce *in press*: Higgins 1961), and *G. girtyi girtyi* ranges from Cu II γ into the Namurian (Bischoff 1957), although Meischner (*G. girtyi* Form A = *G. girtyi girtyi*) restricts it to the Cu III α Zone, with the possibilities of homeomorphic development throughout Cu III. In view of Bouckaert & Higgins' (1963) record of the species from the E_{2a} of the Belgian Dinant Basin and its presence in P₁ and P₂ of the Yoredale succession, the German ranges cannot be used as the basis of correlation. The absence of the gnathodids, *G. semiglaber* and *G. texanus*, as well as species of the genus *Polygnathus*, from this Lower D₂ Subzone indicates that it is younger than Cu II γ .

Meischner (1962: 31) has shown that *G. girtyi simplex* (*G. girtyi* Form B of Meischner) first occurs very near the base of Cu III β , while *G. homopunctatus* occurs just below the base of Cu III β . Thus the upper boundary of the *Mestog-*

nathus beckmanni–*Gnathodus bilineatus* Zone appears to be at the base of the Cu III β Zone, the zone being confined to Cu III α .

The fauna resembles that of the St. Louis Limestone, and has a very close similarity to that of the overlying St. Genevieve Formation.

The base of D₂ in the Avonian is within the *Gnathodus bilineatus*–*Cavusgnathus charactus* Assemblage Zone of North America. *G. bilineatus* first appears in the base of this zone in the Mississippi Valley, but the details of this North American zone are not yet fully studied (Collinson, Scott & Rexroad 1962 : 25). The species first appears in the higher part (Unit C) of the Pella Formation of Iowa (Rexroad & Furnish 1964).

One anomalous aspect of this correlation is the reported first appearance of the *Gnathodus girtyi* group at the top of this zone in the Mississippi Valley (Collinson, Scott & Rexroad 1962 : 25).

The *Gnathodus monodosus* Zone includes the last appearance of *M. beckmanni*, which is last found in the Middle Cu III β of Germany (Meischner 1962). The fact that our zone is established on the basis of a new species makes more precise correlation difficult. *G. nodosus*, which first appears at the base of this zone in the North Crop, first appears in the Middle Cu III β zone of Germany (Meischner 1962).

The overlying *Gnathodus girtyi collinsoni* Zone represents the first appearance of *G. girtyi collinsoni* (= *G. girtyi* Form C of Meischner 1962), which first appears at the base of Cu III γ , in the Middle Rhenaer Kalk of Germany. The last appearance of *G. homopunctatus* on the North Crop falls within this zone, and this is closely similar to its last appearance in Germany (Meischner 1962 : 31, Chart 10). The overall aspect of this Avonian Zone is similar to that of the pre-Middle Glen Dean Chesterian Formations of the Mississippi Valley.

(ii) France and Belgium

There are no adequately illustrated accounts of the Lower Carboniferous faunas of France or Belgium, and our comparisons are made on the basis of published faunal lists. We have not been able to study the original specimens, and our correlations are, therefore, tentative and provisional.

Conil, Lys & Mauvier (1964) have studied the conodont faunas of the Tournaisian and Viséan in Belgium and France. They showed that *Taphrognathus* (synonymous with *Patrognathus* gen. nov. or *Clydagnathus* gen. nov.) occurs in beds that are of Tn_{1a}–Tn_{2b} age. Associated with *Taphrognathus* in Tn_{1b} are *Polygnathus inornatus*, *Pseudopolygnathus dentilineatus*, *Elictognathus costatus* and *Siphonodella obsoleta*, a fauna which is closely similar to that of the Upper K Zone. In Tn_{2b} *Siphonodella duplicata*, *Siphonodella lobata* and *Siphonodella quadruplicata* appear, whilst in Tn_{2c} *Siphonodella sexplicata* makes its first appearance.

Tn_{2c} is characterized by the presence of the genera *Pseudopolygnathus*, *Siphonodella* and *Elictognathus*. The base of Tn_{2c} would appear to correlate with the upper part of the Middle Hannibal Formation of North America, based on the first occurrence of the species *Siphonodella cooperi* and *Siphonodella sexplicata*.

At the base of Tn_{3a} in Belgium and France, the following species have their first

occurrence : *Gnathodus commutatus*, *Gnathodus delicatus*, *Gnathodus semiglaber* and *Polygnathus communis*. *Siphonodella obsoleta* and *Siphonodella duplicata* are also present.

In the Avonian *Gnathodus delicatus* first appears in Z₁. It is followed in the Lower Z₂ Subzone by *Gnathodus simplicatus* and in the upper part of Z₂ by *Gnathodus semiglaber*. Thus the upper part of Z₁ and the Z₂ Subzone would appear to be broadly equivalent in age to Tn_{3a}. There are, however, two peculiarities in the Franco-Belgian Tn_{3a} conodont fauna : firstly, the late first occurrence of *Polygnathus communis*, and secondly, the occurrence of *Pseudopolygnathus triangulus inaequalis*.

Tn_{3b} is characterized in the Franco-Belgian Province by the presence of *Gnathodus delicatus*, *Polygnathus communis*, *Doliognathus excavatus*, *Scaliognathus anchoralis*, *Hindeodella segaformis*, *Gnathodus bilineatus*, *Gnathodus homopunctatus* and *Gnathodus girtyi*.

In Germany two of these species, *Scaliognathus anchoralis* and *Hindeodella segaformis*, and also one of the genera, *Doliognathus*, are confined to the *Scaliognathus anchoralis* Zone (Cu II β/γ). *Gnathodus delicatus* first appears at the base of the *anchoralis* Zone. The youngest occurrence of *Polygnathus communis* is within the *anchoralis* Zone. *Gnathodus homopunctatus* is present at the top of the zone, as too is *Gnathodus girtyi*.

Gnathodus bilineatus in Germany does not appear until after the youngest stratigraphic occurrence of *Scaliognathus anchoralis* (the *anchoralis*-*bilineatus* interval). In the Franco-Belgian Province, on the other hand, the first appearance of the two species is contemporaneous.

In the Franco-Belgian Province the youngest stratigraphic occurrence of the genus *Siphonodella* coincides with the oldest stratigraphic occurrence of the genus *Scaliognathus* at the base of Tn_{3b}. In Germany *Siphonodella* extends into Cu III α in the Hartz Mountains of the Sauerland (Voges 1959). It extends into the same zone in Spain (Dr W. Ziegler, personal communication), but in North Africa (Dr G. Bischoff, personal communication) it is limited to Cu II. The Genus *Elictognathus* became extinct a short distance beneath the *anchoralis* Zone, at the base of the upper *Siphonodella crenulata* Zone (Middle Cu II α), whereas, in the Franco-Belgian Province, the latter genus became extinct at the base of Tn_{3a}. Dr S. C. Matthews is at present investigating the distribution of the *anchoralis* Zone fauna in Europe.

In North America the base of the Sedalia Formation is an unconformity and the genera *Elictognathus* and *Siphonodella* have their youngest stratigraphic occurrence at the top of the Upper Chouteau Formation. *Scaliognathus anchoralis* first appears at the base of the Sedalia Formation. At the base of the Fern Glen Formation the genera *Doliognathus*, *Staurogathus* and *Bactrogathus* first appear. *Gnathodus delicatus*, *Gnathodus* cf. *girtyi*, *Gnathodus semiglaber*, *Gnathodus cuneiformis* and *Gnathodus antetexanus* also are present above the base of the Sedalia Formation.

In Germany there is a gap in the known conodont sequence beneath the *anchoralis* Zone. It appears likely, however, that Tn_{3b} of the Franco-Belgian succession is equivalent in age to the German Cu II β/γ *anchoralis* Zone and the Cu II δ *anchoralis*-*bilineatus* interval combined. It also correlates with the Fern Glen and Burlington

Formations of North America. *Pseudopolygnathus dentilineatus* of Conil *et al.* in Tn_{3b} is synonymous with *Pseudopolygnathus multistriatus* of Mehl & Thomas in the U.S.A.

This would also suggest that the Tournaisian-Viséan boundary in the cephalopod facies of Germany should not be drawn as at present at the top of Cu II α , but higher in the succession at the top of Cu II.

There are, however, two complications. Firstly, the type fossil of the Cu II α horizon, *Pericyclus princeps*, although never recorded from Germany, is recorded from the Tn_{3c} horizon of Belgium. Secondly, *Pseudopolygnathus triangulus inaequalis* is confined to Tn_{3a} in the Franco-Belgian Province and to the middle of the Cu I in Germany. This might imply that the German Upper Cu I and Cu II α horizons are equivalent in terms of the Franco-Belgian Tournaisian to the bedding plane boundary of Tn_{3a}-Tn_{3b}, but we have some reservations about the general applicability of the subspecies of *Ps. triangulus* established by Voges.

In Britain none of the genera *Scaliognathus*, *Staurogathus*, *Doliognathus*, or *Bactrogathus* have been found in the Avonian, although Matthews (1961) did record *Scaliognathus anchoralis*, *Hindeodella segaformis* and *Doliognathus latus* from the Lower Carboniferous in East Cornwall. Thus these fossils, characteristic of the *anchoralis* Zone in Germany were present in the British Lower Carboniferous seas. One possible explanation of their non-appearance in the Avonian is that the *anchoralis* Zone of Germany is represented in the Avonian by the Z₂ Fish Bed, which would thus represent a considerable non-sequence.

Alternatively *Scaliognathus anchoralis* and its typical zonal associates may be limited in their distribution, either by facies or geography. This is supported by the fact that in North America, from which it was first described, *S. anchoralis* is known only from Branson & Mehl's type specimen, and further intensive sampling of the type locality by Dr. C. W. Collinson has failed to produce even one additional specimen (personal communication). It does not seem to be present in Australia, although it is abundant in Germany, France, Belgium, Spain and North Africa. Some of the typical associated genera display similar anomalies in distribution. *Doliognathus* is abundant in some sections in Germany, but absent in others, even though its zonal associates are present in both. It may be that this group of rather bizarre genera are components of one or more natural conodont assemblages of limited tolerance. If this alternative explanation is correct, the *anchoralis* Zone of Germany may be represented not by a hiatus but by a succession with a different fauna in the Avonian. The exact limits of correlation are difficult to determine, but would lie within the Upper Z to Lower C Zones.

It seems possible, however, that the *anchoralis* horizon is equivalent to the lower part of the *Caninia* Dolomite of the Avon Gorge, which has yielded no conodont faunas.

VI. SYSTEMATIC PALAEOLOGY

The following section contains descriptions of the species recorded in the present study. The ranges recorded in the descriptions refer to sample numbers that are listed on p. 292.

The following prefixes are used to describe the various collecting areas :

Avon Gorge : the section at the Avon Gorge, Bristol, and immediately adjacent areas (see p. 18 and Figs. 59-69).

North Crop : the northern limb of the synclinal structure of the South Wales Coalfield in Brecknockshire and Monmouthshire (see p. 22 and Figs. 7, 70-73).

Scotland : the various sections from the Midland Valley of Scotland (see p. 29 and Figs. 79-91).

Farlow : the Avonian section at Farlow, Shropshire (see p. 25 and Figs. 74-75).

In numbers of cases we have made use of open nomenclature in our specific and generic assignments. We have followed this method where either the preservation or numbers (or both) of specimens were so poor that we felt it unjustifiable to use a formal name, even though we have sometimes recognized particular forms as representing new species, and, in two cases, new genera.

Ranges for species are given only for the Avon Gorge and North Crop, except where species are not present in these areas. Ranges for other areas are shown on the appropriate range charts. In all cases, the ranges represent the maximum distribution of the species, which may not always be present in every sample residue between its first and last appearance. In most such cases, its absence is attributable to particular samples proving barren or producing very low yields.

Catalogue numbers refer to specimens deposited in the British Museum (Natural History).

Genus *ANGULODUS* Huddle 1934

1934 *Angulodus* Huddle : 76.

TYPE SPECIES. *Hindeodella walrathi* Hibbard 1927.

Angulodus walrathi (Hibbard)

Plate 29, fig. 8

1927 *Hindeodella walrathi* Hibbard : 205, text fig. 4a, b.

1934 *Angulodus walrathi* (Hibbard) Huddle : 77, Pl. 4, fig. 15 ; Pl. 10, fig. 5.

1934 *Angulodus demissus* Huddle : 77, Pl. 10, fig. 15.

1940 *Angulodus elongatus* Stauffer (*partim*) : 419, Pl. 58, figs. 1, 2 only.

non 1957 *Angulodus walrathi* (Hibbard) Bischoff : 17, Pl. 5, figs. 44, 45.

non 1961 *Angulodus walrathi* (Hibbard) Higgins : 10, fig. 16.

MATERIAL. 21 specimens : figured, X 36.

RANGE. North Crop KL 3-ZLA 6, Avon Gorge Z 4-Z 37.

DESCRIPTION. An arched elongated unit, with a straight anterior bar which is laterally compressed and deflected through 45° in a vertical plane. The anterior bar bears a series of at least 6 fine, laterally compressed, confluent, posteriorly inclined denticles, their apices being discrete. The apical denticle is about twice as high and three times as wide as the other denticles, and is of the same general form. The

posterior bar is about three times longer than the anterior bar and up to twice as deep. The denticles are fine, laterally compressed, needle-like, fused for about half their length, and posteriorly inclined at about 60° to the horizontal in the anterior third. In the posterior portion, the inclination tends to increase, so that in the recurved posterior terminus of the bar, the denticles lie parallel to the main posterior bar. The denticles of the posterior bar tend to have a hindeodellid arrangement. The posterior bar bears up to 23 denticles, about 18 of which lie anterior to the recurved posterior terminus. It has a straight aboral edge in the posterior two-thirds. The basal cavity is small and confined to the area immediately anterior to the apical denticle.

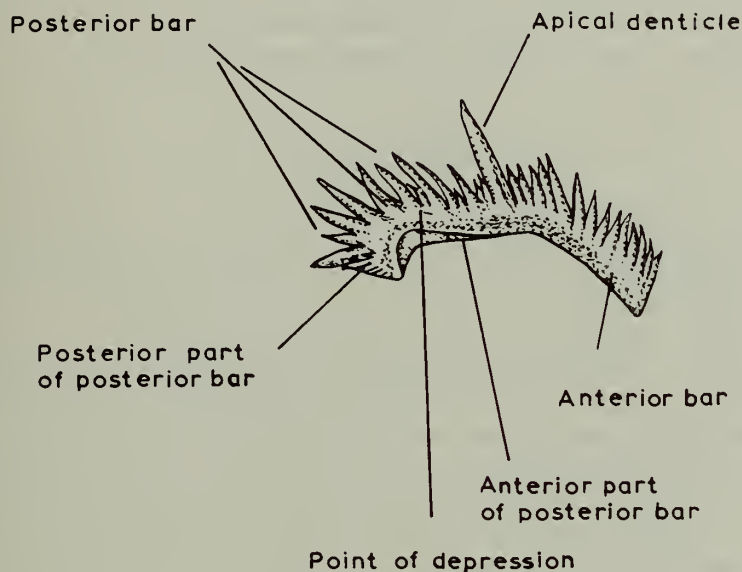


FIG. 17. *Angulodus* sp. showing morphological terms used in the text.

Angulodus sp. nov. B

Plate 29, figs. 5a, b

MATERIAL. 8 specimens : figured, X 37.

LOCALITY AND HORIZON. North Crop, River Clydach, Nr. Gilwern, upper part of Lower Z Zone. Sample ZLA 14.

RANGE. North Crop ZLA 8–ZLA 14, Avon Gorge Z 34–C 7.

DESCRIPTION. An *Angulodus* with robust bar, the short anterior portion being depressed and deflected. Posterior bar up to five times as long as anterior, with 90° posterior depression. Stout discrete denticles.

The whole unit is robust. The bar bears rather rounded lateral faces, and lacks any conspicuous lateral compression. The unit is depressed downward at both the

posterior and the anterior extremities. The apical denticle is of the same size as the denticles of the anterior bar. The anterior bar is short, depressed downward through 70° and deflected inward up to 90° . It bears isolated sub-circular denticles, which tend to increase in size anteriorly. The posterior bar is about four to five times as long as the anterior bar. It is deflected through about 90° at its posterior termination, and bears irregular, isolated, sub-circular denticles, which increase in size posteriorly to the point of depression, when they decrease in size towards the posterior end. Those in the anterior portion of the posterior bar bear smaller denticles (about one third the width of the larger ones) between them. In aboral view the unit is excavated beneath the apical denticle and possesses an inverted basal cavity over its whole length. Here and elsewhere "inverted" is used to describe a basal cavity with wide flaring opening and more or less restricted internal form (see Lindström 1964). This is visible as a basal flange in lateral view.

Angulodus sp. nov. C

Plate 29, figs. 3a-4c

MATERIAL. 18 specimens : figured, X 38, X 39.

LOCALITY AND HORIZON. North Crop, River Clydach, Nr. Gilwern, K and Lower Z Zones. Sample ZLA 10.

RANGE. North Crop KL 1-ZLA 14, Avon Gorge Z 34-Z 38.

DESCRIPTION. A simple, stout, short unit, with a few stout, isolated denticles ; bars are deflected and depressed in at least two directions on the inner side.

The apical denticle is relatively small, sub-circular in cross-section, posteriorly inclined and continuously curved at various angles towards the inner side. The short, stout anterior bar is deflected through 90° and then depressed downward through 90° . It bears 3 to 4 massive, discrete, sub-circular denticles, which tend to decrease in size distally. The posterior bar is massive and very short, the anterior portion being about equal in length to the anterior bar and only slightly longer than the posterior portion. It is stout, with broadly convex lateral faces, and is slightly twisted. The posterior depression may be strong or gentle, but the distal end is depressed through about 90° in both cases. It bears only 3 to 5 stout, sub-circular, posteriorly inclined, isolated denticles, the largest being at the point of depression.

In aboral view the unit is expanded, the cavity being large and extremely shallow, in some cases approaching an inverted basal cavity ; it is largely confined to the anterior portion of the posterior bar (Pl. 29, fig. 3c).

REMARKS. This is a very unusual form, the only comparable species being *Centrogathodus spurius* Branson & Mehl (1934 : 198). The present specimens differ from this in the relative position of the basal cavity and the lack of an "outer spur". A form described as *Angulodus demissus* Huddle by Bischoff & Ziegler (1957 : 43) is also similar. This latter form, which is not *Angulodus demissus* Huddle, could be the same as our specimens. *Angulodus* sp. C differs from *Angulodus* sp. D in the nature of the posterior termination.

Angulodus sp. nov. D

Plate 29, figs. 1a-2c

MATERIAL. 10 specimens : figured, X 40, X 41.

LOCALITY AND HORIZON. North Crop, River Clydach, Nr. Gilwern, upper part of Lower Z Zone. Sample ZLA 11.

RANGE. North Crop ZLA 8-ZLA 14, Avon Gorge Z 34-Z 38.

DESCRIPTION. A simple bar unit similar to *Angulodus* sp. C but with a longer anterior portion of the posterior bar and a less marked and distinctly denticulated depression of the posterior termination.

The apical denticle is fairly small, sub-circular in cross-section, inclined posteriorly and towards the inner side, so that it does not lie in the same plane as the other denticles or the rest of the unit. The anterior bar is short, massive, deflected through 90° ; horizontal or feebly arched upward and then depressed through 90° . It commonly bears 4 to 5 stout, irregular, isolated, sub-circular denticles, which tend to be tallest in the anterior part. The anterior part of the posterior bar is one and a half to twice as long as the anterior bar. The oral surface bears 3 to 4 discrete pointed denticles, their diameter being about two thirds that of the apical denticle, and their cross-sections sub-circular to biconvex. They are inclined at about 45° to the posterior bar, and are separated by irregular smaller "hindeodellid" denticles. They tend to decrease in size posteriorly towards the point of depression. The posterior part of the posterior bar is depressed at an angle of 90° . It is very short, and its oral surface is limited to a single, large, fang-like denticle. This is strongly laterally compressed, with flat to gently convex lateral faces, and anterior and posterior edges. It lies almost parallel to the anterior part of the posterior bar. The posterior termination of the unit is pointed to sharply spatulate. A minute secondary denticle may be developed on the posterior edge of the most posterior denticle. The basal cavity is confined to the area below the apical denticle. The posterior bar commonly has a very fine aboral keel along its whole length.

In aboral view the sub-apical pit is large and extremely shallow, approaching the form of an inverted basal cavity.

REMARKS. A form similar to this species is described by Bischoff & Ziegler (1957 : 43, Pl. 20, figs. 3, 6) as *Angulodus gravis* Huddle. The holotype of *A. gravis* differs greatly from the specimens figured by Bischoff & Ziegler, but there is a marked similarity between their forms and the present specimens.

Genus *APATOGNATHUS* Branson & Mehl 19341934 *Apatognathus* Branson & Mehl : 201.TYPE SPECIES. *Apatognathus varians* Branson & Mehl 1934*Apatognathus bladus* sp. nov.

Plate 20, figs. 15a-16b

DERIVATION OF NAME. From Latin blade.

DIAGNOSIS. *Apatognathus* in which denticles on anterior bar and apical denticle have very conspicuous anterior and posterior keels developed on edges. They are unusually wide and blade-like. Two largest denticles of anterior bar separated by single denticle from apical denticle. Denticles of posterior bar adjacent to apical denticle are minute. Whole unit sharply depressed at apex and strongly inwardly twisted. Inner lateral faces of both bars bear conspicuous ridges near point of contact with denticles and are flat to concave below these ridges.

MATERIAL. 8 specimens : Holotype X 45, Paratype X 46 (both figured).

TYPE LOCALITY AND HORIZON. North Crop, Craig-y-dinas, Breconshire. Sample CYD 7.

RANGE. North Crop CYD 7.

DESCRIPTION. Anterior bar of unknown length ; it is deep and thin, bearing more than 4 strong, greatly laterally compressed denticles on its oral surface, the largest two being separated from the apical denticle by a single small denticle. The denticles of the anterior bar, as well as the apical denticle, are so strongly laterally compressed that they have strong lateral keels developed on their anterior and posterior edges. The combined width of these keels equals or exceeds the width of the "core" of the denticles. The denticles are basally confluent but are discrete for most of their lengths. They are inclined slightly posteriorly. Below the base of these denticles the apical bar bears a conspicuous longitudinal ledge which is rounded and parallels the oral surface of the bar. Below this ledge the aboral surface is relatively wide and there is a slight ledge developed on its inner lateral face. It is not conspicuously excavated. The apical denticle is strongly biconvex in cross-section but the anterior and posterior edges are conspicuous features on both margins. It is elongated, but is not conspicuously greater in width than the largest denticle on the anterior bar. It is straight and tapers gradually. The posterior bar is only about one-third the depth of the anterior, but it is thicker than it is deep. Its oral surface bears a series of crowded, minute and more or less sharply pointed denticles. In cross-section the posterior bar is more or less quadrate with a sharp longitudinal ridge developed on the upper inner lateral face and a more or less smooth to flat outer lateral face. Its basal surface is the widest part of the bar and is flat. In outer

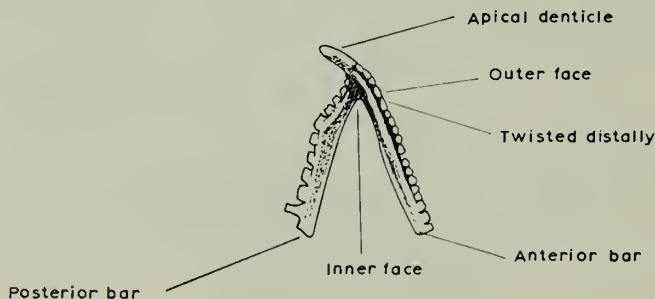


FIG. 18. *Apatognathus* sp. showing morphological terms used in the text.

lateral view the lateral walls of the bar and the denticle faces are flat, and the whole unit is continuously recurved so that all denticles point inward. The slight lateral flange on the outer aboral lateral face of the anterior bar and the wide posterior aboral surface are conspicuous features.

REMARKS. Although our specimens are fragmentary the distinctive size and character of the denticles, as well as the form of the base, appear to set this species apart from all those previously described.

Apatognathus chauliodus Varker

Plate 20, figs. 1a, b, ; 2a, b

1967 *Apatognathus ? chaulioda* Varker : 129, 131, Pl. 17, figs. 1-3, 5.

MATERIAL. 2 specimens : figured, X 44, X 550.

RANGE. Avon Gorge D 7.

DESCRIPTION. The bars diverge at an angle of 25°-35° and in inner lateral view are inclined inwards to slightly face one another. The apical denticle is as wide as the prominent bar cusps, widest at its base and sharply pointed. It is slightly curved and inclined to the posterior. A prominent denticle is present on each of the lateral bars. These bar cusps are equal in size to the apical denticle, but are separated from it by up to 5, but commonly 2 or 3, small compressed denticles, which are shorter in length than the depth of the bar and are fused with one another. The denticles of the bar adapical to the bar cusp may be longer than the height of the bar, and are discrete. The aboral edge of the bar is straight, but the bar itself increases in depth towards the apex from its shortest depth at the adapical extremity. The bar denticles are slightly inclined inwards. The aboral edge of the bars is sharp, an aboral groove is present and the basal cavity beneath the apical denticle is circular.

Apatognathus geminus (Hinde)

Plate 20, figs. 3a-4b, 6a-7b

1900 *Prioniodus geminus* Hinde : 344, Pl. 10, fig. 25.

1928 *Prioniodina ? gemina* (Hinde) Holmes : 19, Pl. 5, fig. 10.

1960 *Apatognathus geminus* (Hinde) Clarke : 4, Pl. 1, figs. 1, 2.

1963 *non Apatognathus ? gemina* (Hinde) Rexroad & Collinson : 7, Pl. 1, figs. 12-17.
(=*Apatognathus scalena* Varker).

MATERIAL. 4 specimens : figured, X 54, X 55, X 56, X 57.

RANGE. North Crop CYD 6-3D 14/15, Avon Gorge C 16.

DESCRIPTION. The most distinctive features of this species are the prominent apical denticle and the large size of two denticles on the anterior bar adjacent to that denticle. The whole unit is strongly recurved and strongly laterally flexed, so that in outer lateral view the aboral surface is visible along almost the whole length of the unit. Both bars are strongly flexed inwards so that the denticles appear to radiate

away from the apical junction. The anterior bar is relatively short and straight with a flat outer lateral face. It bears up to 7 denticles, not including the apical denticle, and these are basally confluent but apically discrete. Their outer lateral faces are strongly convex and they have sharp anterior and posterior edges and they decrease in size towards the anterior tip. The apical denticle is about twice as long as the largest of the denticles of the anterior bar. It is inclined posteriorly and is paralleled by the denticles of the anterior bar; it is straight with a very strongly convex outer lateral face and sharp anterior and posterior edges; it is not expanded on the outer aboral margin. The posterior bar is very slightly shorter than the anterior, and its denticles are conspicuously smaller; they are of more or less subequal height and they are about 7 in number. They are basally confluent but apically discrete with sharp anterior and posterior edges and feebly to gently convex outer lateral faces; these are less conspicuously convex than the faces of the anterior denticles; on the outer lateral aboral margin of the posterior bar there is a more or less conspicuous longitudinal ridge developed parallel to the base. We take this to be the "laterally tumid" character referred to by Clarke (1960). The angle of divergence of the two bars when viewed from the outer lateral side is about 30° - 40° ; they are also strongly flexed inwardly and join each other at an angle of about 40° in the inner lateral view, in such a way that the denticles of the posterior bar are erect and those of the anterior bar point outwards towards the observer. The bars are strongly flexed inward and the denticles curve inward, as well as posteriorly; the denticles of the posterior bar are inclined anteriorly and tend to parallel the main denticle. The inner lateral faces of both the anterior and posterior bars are flat and a rather bevelled aboral edge is developed from them, excavated throughout its length by a narrow, slit-like cavity, which does not increase markedly in size below the apical denticle.

REMARKS. Clarke's illustration of Hinde's specimens makes it clear that the characteristics of the species are the relatively larger size of the denticles adjacent to the apical denticle, and the almost platform-like lateral edges developed on the posterior bar.

Apatognathus petilus Varker

Plate 20, figs. 12a-14b; 17a, b

1967 *Apatognathus petila* Varker: 135, 136, Pl. 17, fig. 11, Pl. 18, figs. 7, 10, 11.

MATERIAL. 23 specimens: figured, X 50, X 51, X 52, X 53.

RANGE. North Crop CYD 7-3D 14/15, Avon Gorge C 7-C 16, D 7.

DESCRIPTION. The orientation of these units is arbitrarily defined by regarding the longer bar as posterior, although the inclination of the apical denticles does not always justify this. *Apatognathus* with slender elongated lateral bars continuously and strongly recurved and flexed; apex of arch formed by them marked by development of 5 large denticles, of which three medial are largest but no single apical denticle is conspicuously larger than rest.

The dental units are slender with a straight, elongated, posterior bar. The posterior bar is about one third longer than the anterior, and has 17-24 crowded denticles, their apices being sharply to bluntly pointed but discrete ; they tend to be more or less uniform in size, though those near the distal end of the bar are slightly smaller than the rest of the series. The inner lateral face of the bar is flat and the base of the aboral edge of the bar when seen in lateral view is straight or very feebly convex.

The posterior bar makes an angle of about 45° with the anterior when seen in lateral view : the posterior bar itself is slightly flexed inwards, although both the distal and proximal thirds are more or less straight.

The anterior bar is shorter than the posterior, and its aboral edge is conspicuously straight. In lateral view it bears a series of crowded denticles which are confluent at their bases but apically discrete, and which have bluntly pointed free tips ; they number up to twelve and increase more or less steadily in size towards the apex. The apex is rounded on the aboral margin and is marked by the development of five rather large and conspicuous denticles, of which the three medial ones are the largest. They are curved inward and sometimes slightly posteriorly, but in most specimens they are more or less erect. They are basally confluent but apically discrete and are biconvex in cross-section, with sharp anterior and posterior edges, and gently convex lateral faces. The largest denticles tend to be large and conspicuous and, when viewed laterally, they tend to radiate from the apex of the arch. There is a slight tendency for the denticles of the posterior bar to increase in size apically. The whole inner lateral face of the unit is continuously recurved, although at any one point on the face the denticles tend to have a flat to only feebly concave surface. In outer lateral view the surface is feebly convex to flat and the aboral margin is marked by a more or less conspicuous ridge, developed on the outer lateral face. The whole aboral cavity is excavated below the apex.

REMARKS. The distinctive features of this species are the general form and curvature of the anterior and posterior bars and the development of the apical denticulation, in which a series of denticles, rather than any individual denticle, are of major size.

Apatognathus porcatus (Hinde)

Plate 31, fig. 27

1900 *Prioniodus porcatus* Hinde : 344, Pl. 10, fig. 26.

1928 *Prioniodus porcatus* Hinde ; Holmes : 22, Pl. 3, fig. 26.

1960 *Apatognathus porcata* (Hinde) Clarke : 5, Pl. 1, figs. 3, 4.

1963 *non Apatognathus ? porcata* (Hinde) Rexroad & Collinson : 8, Pl. 1, figs. 7-11.

MATERIAL. 10 specimens : figured, X 220.

RANGE. North Crop CYD 6-7, Avon Gorge C 9-C 16.

DESCRIPTION. Clarke's diagnosis of this species, as well as his illustration of Hinde's holotype, make it clear that its distinctive features are the relatively uniform size of the denticles, and the very strong bilateral extension of the oral surface of the

anterior bar. This is well shown by the view of the specimen illustrated on Pl. 1, fig. 4 of Clarke. It seems, therefore, that the specimens described by Rexroad and Collinson must be excluded from the species, for in them the anterior bar does not appear strongly laterally expanded. Material from both Scotland and the North Crop representing this species is fragmentary but the anterior bar shows the characteristic very strong lateral expansion.

Apatognathus scalenus Varker

Plate 20, figs. 9a-11b

1963 *Apatognathus* ? *gemina* (Hinde) Rexroad & Collinson : 8-9, Pl. 1, figs. 12-17.

1967 *Apatognathus* ? *scalena* Varker : 136, 137, Pl. 18, figs. 1, 2, 4, 5.

MATERIAL. 10 specimens : figured, X 47, X 48, X 49.

RANGE. North Crop CYD 6-3D 14/15.

DESCRIPTION. The characteristic features of this species are the strong lateral flexing of the anterior bar, the general form of the unit, the development of a strong, elongate, laterally compressed denticle at the apex, an apical angle of about 30° in lateral view, and the development of at least one strong denticle in the medial portion of the posterior bar.

Varker has given a detailed description of this species. The anterior bar is about equal in length to or slightly longer than the posterior. It bears 10-14 laterally compressed, pointed, sharp edged, basally confluent, inwardly curving denticles, which increase in size proximally. The apical denticle is at least two to three times as long as the largest of the remaining denticles ; it has sharp anterior and posterior margins and a convex inner lateral face, the convexity decreasing distally. The posterior bar develops about 10 denticles, of which the one in the medial position is twice as large as its neighbours and slightly larger than that adjacent to the apical denticle. These denticles are rather less closely spaced than those of the anterior bar, and in some of them even the basal surfaces are discrete ; they are sharply pointed and stand more or less erect to the bar, but those nearest the apical denticle are recurved so that they lie more or less parallel to it. The lateral faces of both bars are marked on the inner side by a more or less conspicuous shoulder below the origin of the denticles.

Both bars are twisted laterally and they diverge when viewed orally at an angle of about 30°, as well as being twisted in a horizontal plane, so that in oral view all the denticles radiate away from the apical area.

In outer lateral view a conspicuous longitudinal ridge is developed at about mid-height. In both bars the aboral surface is excavated by a narrow slit-like groove, which is only slightly expanded below the apical denticle.

REMARKS. In some specimens the posterior bar is marked by the development of two conspicuously large denticles, although one of these is always larger than the other.

Apatognathus varians Branson & Mehl

Plate 20, figs. 5a, b

- 1934 *Apatognathus varians* Branson & Mehl : 201, Pl. 17, figs. 1-3.
 non 1939 *Apatognathus ? varians* Branson & Mehl ; Cooper : 385, Pl. 47, fig. 30.
 1944 *Apatognathus varians* Branson & Mehl ; Branson & Mehl in Shimer & Shrock : 402, Pl. 93, figs. 59-61.
 1956 *Apatognathus varians* Branson & Mehl ; Bischoff & Ziegler : 145, Pl. 14, fig. 3.
 1958 *Apatognathus varians* Branson & Mehl ; Klapper : 1085, Pl. 141, figs. 6, 8.
 1961 *Apatognathus varians* Branson & Mehl ; Ethington, Furnish & Wingert : 763, Pl. 90, fig. 11.
 1961 *Apatognathus varians* Branson & Mehl ; Freyer : 36, Pl. 1, fig. 13.
 1965 *Apatognathus varians* Branson & Mehl ; Spasov : 84, Pl. 1, fig. 3.
 1965 *Apatognathus varians* Branson & Mehl ; Ethington : 575.

MATERIAL. 6 specimens : figured X 42.

RANGE. North Crop ZLA 9-ZL 9.

DESCRIPTION. The unit is considerably arched and bowed. The apical denticle is laterally compressed, with convex lateral faces, and sharp anterior and posterior edges. It is inclined posteriorly and laterally towards the inner side. The anterior bar lies in the same plane as the apical denticle, but is twisted inwards distally. It bears at least 20 closely crowded, sub-circular, posteriorly-inclined denticles, their apices being discrete and pointed.

The anterior bar is strongly laterally compressed in its distal third, with flattened lateral faces, but the inner and outer lateral faces become strongly convex in their proximal two-thirds. The posterior bar is short, considerably flexed, about as long as that of the anterior and makes an angle of about 20° with the anterior bar. It is curved inward, and bears denticles similar to those of the anterior bar, but tending to be upright or anteriorly inclined. Both bars decrease in height towards their distal extremities. The basal cavity is minute and situated beneath the apical denticle.

On specimen number X 42 (Plate 20, figs. 5a, b) the inner lateral face of the apical denticle tends to be flat, but the outer lateral face is strongly convex, the inner lateral face of the bars immediately below the apical denticle tending to be rather flattened. The two denticles immediately posterior to the apical denticle tend to be larger than any of those on the anterior bar. The distal portion of the posterior bar is broken. The outer lateral face of the anterior bar is similar in general cross-section to the inner lateral face.

Apatognathus cf. *libratus* Varker

Plate 20, figs. 8a, b

- 1967 *Apatognathus ? librata* Varker : 134, 135, Pl. 18, figs. 3, 6, 8, 9, 12, 13.

MATERIAL. 1 specimen : figured, X 58.

RANGE. Scotland DUN 78.

DESCRIPTION. The characteristic feature of this species is its virtual bilateral

symmetry. In the present specimen the two limbs diverge at an angle of about 45° in outer lateral view. The denticles stand more or less erect to the limbs towards their distal extremities but they tend to radiate away from the apex; they are more or less sub-equal in size and closely similar in size on both anterior and posterior bars. The apical denticle tends to be only slightly larger than the largest on the bars, on which the largest denticles tend to be separated by a single denticle from both the anterior and posterior edges of the apical denticle. The denticles are confluent for about two-thirds of their length, with sharp anterior and posterior edges and gently convex lateral faces. The whole unit is continuously recurved inward and on both the anterior and posterior limbs there is a more or less conspicuous basal longitudinal ridge developed near the aboral margin. In inner lateral view the whole unit is regularly and continuously concave. The bars of the present specimens are of rather unequal length, the anterior bearing 9 denticles and the posterior 8; it is probable that neither is complete, however.

REMARKS. The present specimen bears a very close resemblance to Varker's holotype in all features except the relative size of the apical denticle. In the present specimen this is only about half the size of that in Varker's specimens. This does not seem to us, at present, a valid reason for regarding the two forms as distinct species. Varker notes that the processes of his specimens bear up to 20 or more denticles.

We have used the name of this species as the zonal name for one of our zones. The zone is characterized by the common occurrence of apatognathids, virtually all of which are broken, however. Many of these resemble the present species, but they are too fragmentary to include in the count of material.

Apatognathus sp. nov. A

Plate 31, fig. 22

MATERIAL. 2 specimens: figured, X 43.

TYPE LOCALITY AND HORIZON. North Crop, River Clydach, Nr. Gilwern, Z Zone. Sample ZLA 13.

RANGE. North Crop ZLA 13.

DESCRIPTION. A strongly arched *Apatognathus* with conspicuous apical denticle. Slender recurved anterior bar has about 10 crowded denticles, and is curved in the same plane as the apical denticle. Posterior bar stout, deep, deflected and depressed, with 4-5 large, discrete denticles.

The unit is arched and bowed. The apical denticle is tall, laterally compressed, with knife edges on the anterior and posterior margins, posteriorly recurved and laterally inclined toward the inner side. The outer face is strongly, and the inner face feebly, convex. The anterior bar lies in the same plane as the apical denticle and is shallow and somewhat recurved. It bears about 10 laterally compressed, posteriorly inclined, partially fused denticles. The deep posterior bar is deflected, and depressed. It bears a series of 4 or 5 large, discrete, laterally compressed

denticles, standing perpendicular to the bar, the largest developed at about midpoint. The basal cavity is minute and is situated beneath the apical denticle.

REMARKS. This form is very similar to *Apatognathus? geminus* (Hinde) of Rexroad and Collinson (1963), our specimens differing only in that the posterior bar is more strongly curved and twisted. This may not be specifically significant, and if the two forms are identical, the range of the present form would be extended upward, into the St. Louis Formation of the Upper Mississippi Valley. Rexroad and Collinson (1963 : 7) point out that in North America there is a gap between the Upper Devonian and Upper Viséan record of *Apatognathus*. Our apatognathid fauna appears to bridge that gap, and thus *Apatognathus* may not necessarily be a polyphyletic genus as Rexroad and Collinson suggest.

Apatognathus sp.

Plate 31, fig. 2

MATERIAL. 16 specimens : figured, X 318.

RANGE. Avon Gorge Z 36-D 32.

DESCRIPTION. Fragmentary apatognathids occur in various parts of the succession. The specimen illustrated represents one such form, though other broken specimens show considerable variation. They are not sufficiently complete to make it possible to refer them to individual species.

Genus *CAVUSGNATHUS* Harris & Hollingsworth 1933

1933 *Cavusgnathus* Harris & Hollingsworth : 200-201.

TYPE SPECIES. *Cavusgnathus alta* Harris and Hollingsworth 1933.

DESCRIPTION. Harris and Hollingsworth (1933) gave the following description for the genus : 'This genus is erected to include those lanceolate plated conodonts with no semblance of a median crest in the median oral channel. Outline of plate lanceolate to claviform ; oral face of plate with complete, deep, median longitudinal channel without crest and bordered by marginal rims ornamented with denticles, nodes, corrugations, or combinations of the same ; posterior bar denticulate'.

Ellison (1941) gave the following revised description : 'Elongate platform-like teeth with high sides, extending parapet-like above a median longitudinal trench, one parapet continued into a free longitudinal blade and connected at the posterior end to opposite parapet, whose length is limited by the length of the platform ; aboral surface of platform smooth, deeply excavated as a longitudinally elongate, laterally asymmetrical spathodid-like cup, pointed at each end, transversely by a median longitudinal groove, which extends to the ends of the platform and along the aboral edge of blade ; sides of platform somewhat constricted laterally above the aboral margin, to produce a lip-like lateral margin of variable width ; oral surface of platform more or less grooved transversely, oral edge of blade denticulate and crenulate.

For purposes of description, the blade is directed anteriorly. It is continued posteriorly as the outer edge of platform, the blade parapet. The elevated inner edge of the platform is the inner parapet.'

REMARKS. *Cavusgnathus* bears a marked resemblance to the genus *Mestognathus*, but the two are easily distinguished on the basis of their basal cavities, that of *Mestognathus* being small and narrow and that of *Cavusgnathus* wide and flaring.

The anterior blade in the cavusgnathid group has hitherto been thought to be confined to the outer side of the unit and to be lateral in position (Rexroad in Lindström 1964 : 124). However, the present study has shown that the position of the blade in *Cavusgnathus* varies through the section. In the K Zone it is both medial and lateral in position, whereas in the Z to D Zones it is lateral in position. Some forms in the Z Zone have been found with the blade on the inner side.

In North America it has hitherto been thought that *Cavusgnathus* developed from *Taphrognathus* in the Late Valmeyeran (Rexroad and Collinson 1963). *Cavusgnathus*, however, makes its first appearance in the Avon Gorge in the basal beds of

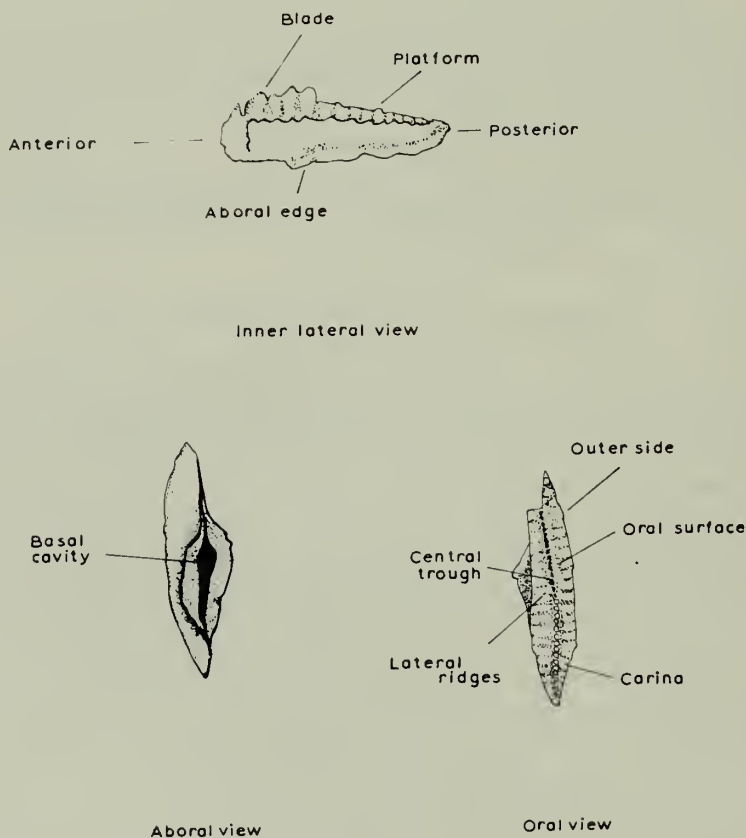


FIG. 19. *Cavusgnathus* sp. showing morphological terms used in the text.

the Z Zone and an earlier origin must therefore be suggested. The writers believe that *Cavusgnathus* may have had its origin in *Spathognathodus plumulus* sp. nov.

Cavusgnathus charactus Rexroad

Plate 13, figs. 6a-7d, 13a-c

1957 *Cavusgnathus characta* Rexroad : 15-16, Pl. 1, figs. 1, 2.

1961 *Cavusgnathus characta* Rexroad ; Rexroad & Collinson : Pl. 1.

1963 *Cavusgnathus characta* Rexroad ; Rexroad & Collinson : 8, Pl. 1, fig. 29.

MATERIAL. 8 specimens : figured, X 59, X 61, X 62.

RANGE. North Crop CYD 7, Avon Gorge S 5-S 44.

DESCRIPTION. The diagnostic characters of this species are the general form of the anterior blade, which consists of six to eight denticles with low rounded apices of more or less uniform size, except for those in the anterior portion. The posterior end of the blade is separated by a distinct undenticulated depression from the outer lateral face of the posterior platform. The free anterior blade is not long in comparison with the length of the platform. In outer lateral view the platform decreases in depth towards the posterior end. Its oral surface is bluntly crenulate and the whole aboral surface of the unit is regularly concave. There is a conspicuous thickening below the basal cavity, which is situated in the anterior portion of the platform and the whole outer lateral edge of the blade is bevelled. In some specimens there are only four or five denticles on the anterior blade, the most posterior being the largest and most massive. They all stand more or less erect to the bar. The oral margin of the platform is continuously convex in outer lateral view, the outer parapet obscuring the inner, when seen in this direction. The blade tends to decrease in depth posteriorly ; its anterior aboral corner is bluntly rounded. In inner lateral view the basal cavity makes a conspicuous flaring feature on the aboral surface, and the oral edge of the platform is strongly convex and irregularly crenulate. The platform tends to show some narrowing anteriorly and its widest point is in the posterior half. In the posterior half there is a median carina of variable length, consisting of a number of rather conspicuous but fused, strongly laterally compressed nodes. The carina extends beyond the posterior limit of the platform proper. The platform edges are decorated with feeble transverse ridges and the whole median area of the platform is excavated by a deep U-shaped trough, which runs parallel to the anterior blade and does not decrease greatly in depth when traced anteriorly.

In aboral view the aboral cavity is widely flaring and asymmetrical, but the basal pit itself is restricted to the anterior quarter of the platform. It is deep but not very broad and is extended as a longitudinal slit to the posterior end of the unit, the lateral edges of the lip gradually converging towards the posterior end. It is also extended anteriorly for a short distance, though the inner lateral lip, when seen in aboral view tends to be more widely flared than the outer, and also in some, though not in all, specimens to extend further forward.

The total length of the blade is about one-third of the whole length of the unit. The blade is free for about half its length.

REMARKS. In some specimens there is a slight asymmetry of the posterior platform, the inner lateral posterior margin tending to be more strongly outflexed than the outer. The platform is widest on its oral edge and, especially in its posterior half, tapers rapidly towards its aboral margin.

Cavusgnathus convexus Rexroad

Plate 14, figs. 2a-d

- 1957 *Cavusgnathus convexa* Rexroad : 17, Pl. 1, figs. 3-6.
 1958 *Cavusgnathus convexa* Rexroad ; Rexroad : 16, Pl. 1, figs. 12-14.
 1961 *Cavusgnathus convexa* Rexroad ; Rexroad & Collinson : Pl. 1.
 1964 *Cavusgnathus convexa* Rexroad ; Rexroad & Furnish : 670, Pl. 111, fig. 1.
 1965 *Cavusgnathus convexa* Rexroad ; Rexroad & Nicoll : 17, Pl. 1, figs. 14, 15.

MATERIAL. 5 specimens : figured, X 63.

RANGE. Avon Gorge S 20-S 41, North Crop 3D 13.

DESCRIPTION. The margins of the inner and outer parapet are straight. A deep trough runs the length of the platform and occasionally a few nodes form a carina at its posterior extremity. The parapets are ornamented by regularly spaced, transverse ridges. In lateral view, the anterior blade is seen to consist of six laterally compressed denticles, which are fused nearly to their apices. The anterior blade is highest near, but not at, its posterior extremity and this gives the blade a convex oral edge. The anterior blade, which is less than one third the total length of the unit, is free for half its length. The oral edge is convex and the aboral edge is straight to slightly arched. The posterior edge is rounded. The basal cavity is of moderate depth and asymmetrical ; it is long, extending for two thirds the length of the unit, and reaches the posterior extremity of the unit. The inner is more flared than the outer. A keel runs from the anterior edge of the basal cavity to the anterior extremity of the unit.

Cavusgnathus cristatus Branson & Mehl

Plate 14, figs. 3a-d

- 1940 *Cavusgnathus cristata* Branson & Mehl : 177, Pl. 5, figs. 26-31.
 1947 *Cavusgnathus cristata* Branson & Mehl ; Cooper (*partim*) : 91, Pl. 20, figs. 4-6 ;
 (non Pl. 20, figs. 7-10).
 1953 *Cavusgnathus cristata* Branson & Mehl ; Hass : 77, Pl. 14, figs. 12-14.
 1956 *Cavusgnathus cristata* Branson & Mehl ; Elias : 115, Pl. 11, figs. 1-6.
 1956 *Cavusgnathus cristata* var. *grandis* Elias : 115, Pl. 11, figs. 12-14.
 non 1957 *Cavusgnathus cristata* Branson & Mehl ; Bischoff : 19, Pl. 2, figs. 7a, b. (= *C. naviculus*).
 1958 *Cavusgnathus cristata* Branson & Mehl ; Rexroad : 16, Pl. 1, figs. 15-17.
 1961 *Cavusgnathus cristata* Branson & Mehl ; Rexroad & Burton : 1151, Pl. 138, fig. 16.
 1961 *Cavusgnathus cristata* Branson & Mehl ; Rexroad & Collinson : Pl. 1.

MATERIAL. 8 specimens : figured, X 64.

RANGE. Avon Gorge D 26, North Crop 3D 14/15-3D 22.

DESCRIPTION. The margin of the outer parapet of the platform is straight and that of the inner parapet, convex. A deep trough is developed for the greater part of the length of the platform, except for the posterior quarter of the platform, where there is a short carina, which bears a few nodes. The platform is ornamented by a number of transverse ridges of medium length, which extend into the trough. In oral view the flaring of the basal cavity on its inner side is seen.

The anterior blade, which rises out of the outer parapet, slopes slightly towards the anterior. The posterior three denticles of the anterior blade are highest. The anterior edge of the anterior blade and the posterior edge of the platform are of equal elevation. Half the length of the anterior blade is free. Aborally, the basal cavity is asymmetrical and flared, there being a greater flare on the inner side than on the outer.

REMARKS. This species closely resembles *Cavusgnathus convexus* but differs from the latter in that the basal cavity does not extend to the posterior extremity of the unit. In addition *C. convexus* rarely bears a carina and has fewer and shorter ridges in the surface ornamentation.

The present specimens show an even closer similarity to *C. regularis* Youngquist & Miller (as interpreted by Rexroad & Nicoll 1965, Pl. 1, figs. 16, 17) and this species may be a junior synonym of *C. cristatus* Branson & Mehl.

Cavusgnathus naviculus (Hinde)

Plate 13, figs. 12a-d. Plate 14, figs. 1a-d, 4a-6d

- 1900 *Polygnathus navicula* Hinde : 342, Pl. 9, fig. 5.
 1928 *Polygnathus navicula* Hinde ; Holmes : 18, Pl. 7, fig. 14.
 1947 *Cavusgnathus cristata* Branson & Mehl ; Cooper (*partim*) : 91, Pl. 20, figs. 7-10.
 1957 *Cavusgnathus cristata* Branson & Mehl ; Bischoff : 19, Pl. 2, figs. 7a, b.
 1960 *Cavusgnathus navicula* (Hinde) Clarke : 23, Pl. 4, figs. 1-3.
 1960 *Cavusgnathus inflexa* Clarke : 23, Pl. 3, figs. 17, 19.
 1961 *Cavusgnathus navicula* (Hinde) Rexroad & Burton : 1151, Pl. 139, figs. 4-13.
 1965 *Cavusgnathus navicula* (Hinde) Rexroad & Nicoll : 17, 18, Pl. 1, figs. 24, 25.

MATERIAL. 9 specimens : figured, X 65, X 66, X 67, X 68, X 69.

RANGE. North Crop 3D 22, Avon Gorge D 26.

DESCRIPTION. Unit slender and elongate in lateral view with short blade ; long, tapering inner and outer lateral sides which are almost straight in oral view, and are about two to three times as long as the blade. In oral view they are abruptly tapered in their posterior quarter, and the lateral edges are finely serrated. The oral surface is decorated by transverse lateral ridges, which converge, but do not meet, towards the narrow, shallow central trough. This trough is deepest in the anterior third ; on the inner lateral oral surface the ridges are obsolescent and are replaced by rounded nodes. There are about 10 transverse ridges on the outer lateral face. In the posterior third of the unit there is the development of a rather inconspicuous carina, consisting of fine, elongate, node-like denticles joined by a thin median ridge. The inner lateral aboral flange is conspicuous in oral view.

In outer lateral view the unit is characterized by a rather straight median portion of more or less even depth, both the oral surface and to a lesser extent the aboral surface appearing straight-edged in lateral view. The basal apron of the outer lateral margin is considerably less flared and deep than that on the opposite lateral margin.

The anterior blade decreases rapidly in depth anteriorly and its aboral edge, though straight, is depressed vertically. It bears about six oral denticles, of which only the most posterior are conspicuous, the largest being the most posterior of the series. The oral edge is bluntly crenulate and the whole outer lateral face is gently convex or flat, the junction with the aboral edge below the main denticle being concave. The posterior end of the unit is gently downflexed and the posterior aboral terminus is bluntly spatulate in lateral view.

The posterior platform decreases in width towards the posterior end, the decrease being especially prominent in its posterior quarter. The anterior edge of the anterior blade falls sharply away in its anterior third, so that the anterior is vertical, but is still minutely denticulate. In inner lateral view the most prominent feature is the large, rounded, depressed apron above the aboral margin of the cavity. This occupies about half the total length of the unit and is regularly and strongly convex.

In aboral view the cavity is also a conspicuous feature. The anterior half is wider than the posterior, the anterior point of origin being below the apical denticle. The point of maximum width is about one-third of the total length from the anterior end and the cavity is terminated posteriorly about five-sixths of the total length of the unit from the anterior end, so that the posterior aboral edge of the unit is blade-like. The anterior aboral edge of the blade is also thin.

Cavusgnathus unicornis Youngquist & Miller

Plate 31, figs. 13a, b

- 1949 *Cavusgnathus unicornis* Youngquist & Miller : 619, Pl. 101, figs. 18-23.
 1947 *Cavusgnathus cristata* Cooper (*partim*) : 91, Pl. 20, figs. 7-10 only.
 1957 *Cavusgnathus unicornis* Youngquist & Miller ; Rexroad : 17, Pl. 1, fig. 7.
 1957 ? *Cavusgnathus unicornis* Youngquist & Miller ; Lys & Serre : 1042, Pl. 2, figs. 3a, b.
 1958 *Cavusgnathus unicornis* Youngquist & Miller ; Rexroad : 17, Pl. 1, figs. 6-11.
 1961 *Cavusgnathus unicornis* Youngquist & Miller ; Rexroad & Burton : 1152, Pl. 138, figs. 10-12.
 1961 *Cavusgnathus unicornis* Youngquist & Miller ; Rexroad & Collinson : Pl. 1.
 1963 *Cavusgnathus unicornis* Youngquist & Miller ; Rexroad & Collinson : 9, Pl. 1, figs. 26-27.
 1964 *Cavusgnathus unicornis* Youngquist & Miller ; Rexroad & Furnish : 670, Pl. 111, fig. 6.
 1965 *Cavusgnathus unicornis* Youngquist & Miller ; Rexroad & Nicoll : 18, Pl. 1, figs. 18-20.

MATERIAL. 131 specimens : figured, X 329.

RANGE. North Crop CYD 6-3D 14/15, Avon Gorge C 34-D 26.

DESCRIPTION. The most distinctive feature of this species is the conspicuously large posterior denticle of the anterior blade.

In aboral view the cavity is a conspicuous feature of the unit. It tends to be

asymmetrical in detail, the inner side being rather wider than the outer, and sometimes starting a little anteriorly to the outer. The widest part of the cavity occurs in the anterior third. It is extended posteriorly as a narrow, elongate pointed cavity. It is deepest in its anterior half.

In oral view the unit tapers regularly towards the posterior end, the narrowing being especially conspicuous in the posterior fifth. It is widest near the position of the largest denticle on the anterior blade and its sides are more or less straight, though in a few specimens they may be gently convex. The inner and outer parapets are ornamented by a number of transverse, parallel, straight ridges, which tend to be node-like in younger forms. They are most strongly developed in the anterior half and are relatively short, not reaching the broad, shallow, concave trough, which extends along the median part of the platform. There is a tendency for a slight central carina with two or three nodes to develop in the posterior one-fifth or one-sixth of the unit. There is a very conspicuous median depression on the inner side of the anterior blade and the inner anterior margin of the platform is strongly deflected inwards. In lateral view the oral and aboral edges are gently convex and the outer parapet is very slightly higher than the inner.

The anterior blade slopes sharply downward from the largest denticle on the posterior end. Its anterior aboral margin is bluntly spatulate and it bears a series of inconspicuous node-like serrations along its length. These tend to gradually increase in size towards the posterior end, the posterior denticle being enormously expanded. It is not very high, but it is greatly elongated antero-posteriorly, so that it resembles a shark fin, with a convex anterior edge and a straight or concave posterior edge. It is bluntly pointed, with more or less flat lateral faces and blunt anterior and posterior edges. The overall profile of the anterior blade may be gently convex or straight. It is about one-third the total length of the unit, but only about half of it is actually free of the platform. The anterior and posterior edges of the unit are almost vertical.

REMARKS. Rexroad (1958) remarked on the changes which occurred during ontogeny. Similar ontogenetic changes have been noted in the present study. The young specimens tend to be narrow, with parapets which are nearly straight. In more mature specimens the platform broadens without a corresponding increase in length and the flare of the inner lip of the basal cavity also increases. The number of small denticles on the anterior blade, anterior to the prominent posterior denticle, also increases. A feature of the juveniles, which Rexroad did not note, was their tendency to develop a row of nodes on the parapet, rather than ridges.

Cavusgnathus unicornis resembles *C. charactus* and *C. convexus* in the convex outline of the platform in lateral view. However *C. unicornis* is distinctive because of the high posterior denticle of the anterior blade.

There is a tendency in some specimens for the outer lateral face to be offset near the position of the largest denticle. The carina in the posterior portion of the platform seems to occur only in the largest individuals.

Young individuals of this species from the present faunas agree with Rexroad's description (1958 : 17). Older individuals in our D collections have been identified

by Dr. Rexroad as *C. naviculus*. We suspect that *C. unicornis* may be synonymous with *C. naviculus*.

Cavusgnathus ? sp. nov. A

Plate 9, figs. 10a-d

MATERIAL. 2 specimens : figured, X 70.

LOCALITY AND HORIZON. North Crop, ZLA 32.

RANGE. North Crop ZLA 32.

DESCRIPTION. A cavusgnathid with the anterior blade developed on the left side when viewed from the posterior.

The unit is highly reminiscent of species referable to the genus *Cavusgnathus* but the free blade is developed on the opposite side, that is, the left side, when viewed from the posterior. The platform is long, sinuous and deep, being ornamented by transverse ridges which become obsolescent towards the deep median trough. The trough is sinuous, deep, deepening towards the anterior, with a suggestion of a carina filling it near the posterior termination. The blade is broken, but can be seen to be situated on the opposite side of the platform to known cavusgnathids ; it appears to be high and formed of laterally compressed denticles.

In aboral view the basal cavity occupies the whole platform area, the lips being flared, especially on the blade side, and on the posterior part of the non-bladed side.

REMARKS. All known species of *Cavusgnathus* are asymmetrical units, the lateral blade being found on one side only and no mirror images being known (Rexroad in Lindström 1964 : 124). The above form is, in fact, a mirror image of a typical individual of the genus *Cavusgnathus*.

Genus *CLYDAGNATHUS* gen. nov.

DERIVATION OF NAME. From the River Clydach.

DIAGNOSIS. A lanceolate, curved platform unit, with short anterior blade, an elongate platform and medial trough. The blade is medial to lateral ; the platform is ornamented and may bear a posteriorly restricted carina ; basal cavity asymmetrical. The phylogenetic origin and stratigraphic range are described below (p. 85).

TYPE SPECIES. *Clydagnathus cavusformis* gen. et. sp. nov.

DESCRIPTION. The blade is medial to lateral, short, and slopes anteriorly. The platform is lanceolate, elongated, bowed and laterally curved. It bears variable marginal ornament, ranging from nodes to transverse ridges. A medial trough is present, except at the posterior end, where a short medial carina is sometimes present which occasionally extends beyond the platform as a posterior blade. The asymmetrical cavity is expanded, but is medially situated beneath the platform. The unit is not grooved.

REMARKS. This genus is closely allied to *Scaphignathus* and *Cavusgnathus*.

Many adult specimens of *Scaphignathus* (illustrated by Helms 1959) have a similar appearance to juveniles of *Clydagnathus*. The present genus can be distinguished by the lack of a carina on the oral surface of the platform (except at the posterior extremity) and the distinct basal cavity. *Clydagnathus* can be distinguished from *Cavusgnathus* by the general anterior closure of the oral trough, by the merging of the marginal ornament with the blade, and by the lateral, rather than longitudinal, expansion of the cavity. It is thought that *Clydagnathus* was derived from *Spathognathodus plumulus plumulus* by addition of nodes and lateral movement of the blade. *Scaphignathus* probably arose from a polygnathid ancestor and *Cavusgnathus* was derived from *Taphrognathus* (Rexroad and Collinson 1963). Thus none of the three broadly homoeomorphic genera *Scaphignathus*, *Clydagnathus* and *Cavusgnathus* is related genetically and their different positions in the stratigraphical column justify the use of distinct generic nomenclature. The use of distinct generic names is a reflection of their distinct phylogenetic origin as well as an aid to stratigraphy, although the degree of morphological difference between them is less than that between most other platform genera.

Clydagnathus cavusformis sp. nov.

Plate I, figs. 9-13d

DERIVATION OF NAME. From the close resemblance to the genus *Cavusgnathus*.

DIAGNOSIS. Clydagnathid with lateral anterior blade very short, plume-like and sub-triangular in lateral profile, consisting of about four to six fused denticles with free, bluntly chevron shaped tips, largest near the posterior end.

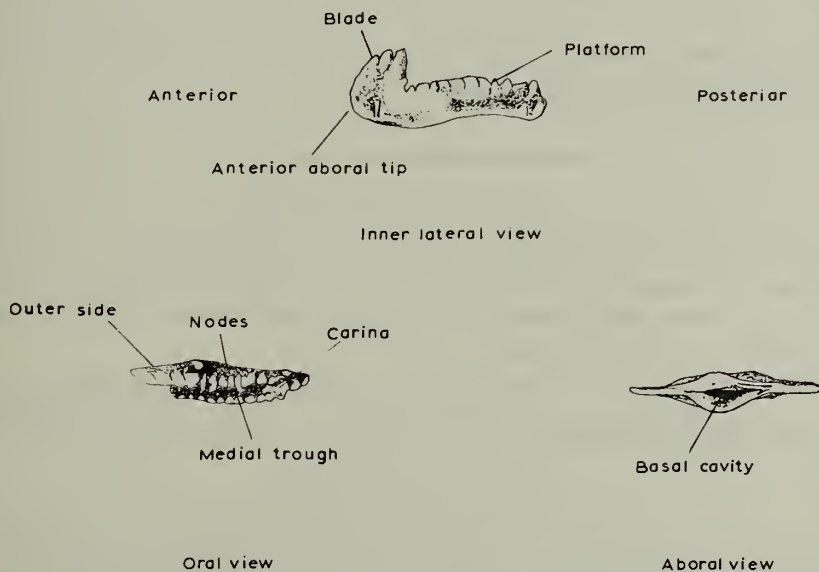


FIG. 20. *Clydagnathus* sp. showing morphological terms used in the text.

MATERIAL. 20 specimens : Holotype X 75, Paratypes X 71, X 72, X 73, X 74 (all figured).

TYPE LOCALITY AND HORIZON. R. Clydach, Nr. Gilwern, K Zone. North Crop. Sample KL 5.

RANGE. North Crop KL 1–KL 12, Avon Gorge K 12–K 17.

DESCRIPTION. The blade is short, being only a quarter to a fifth the length of the platform. It is lateral in position, sub-triangular in profile and bears 4 to 9 fused, erect denticles with distinct apices. The largest denticle of the anterior blade is near the posterior end. The anterior aboral tip is bluntly spatulate. The platform is long and rather pointed, bearing lateral nodes separated by a medial trough, which usually deepens anteriorly (e.g. Pl. 1, fig. 11). In adult specimens the lateral ridges may coalesce medially, to form a sharply sinuous longitudinal ridge in the posterior portion, the medial trough then being confined to the anteriormost portion of the platform (e.g. X 72, Pl. 1, fig. 9). In other specimens the lateral ridges may be continuous across the platform dividing it into a series of isolated laterally elongated troughs (e.g. X 73, Pl. 1, fig. 10), with a more or less prominent longitudinal marginal ridge on one side. The platform may be very slender, elongate and sinuous (e.g. X 74, X 75, Pl. 1, figs. 13, 11). The posterior part may bear a short restricted carina of rounded, isolated nodes (e.g. X 75, Pl. 1, fig. 11) which can be produced as a short posterior blade. The inner oral rim of the platform is deflected through 80°, at the anterior end, so preventing the trough from opening anteriorly.

The cavity is large, asymmetrical with thickened lips and is conspicuously laterally expanded.

REMARKS. This species is closely related to *C. gilwernensis*, from which it differs by having a lateral blade rather than a medial one. It can be distinguished from the genus *Cavusgnathus* by the closed medial trough and the pseudopolygnathid type of asymmetrical sub-circular basal cavity.

Clydagnathus darensis sp. nov.

Plate 2, fig. 6a–7d

DERIVATION OF NAME. From the type locality at Daren Ddu.

DIAGNOSIS. Clydagnathid with relatively low, short anterior blade, consisting of 4 or 5 more or less erect denticles, those at the anterior end being only slightly smaller than those at the posterior.

MATERIAL. 23 specimens : Holotype X 77, Paratype X 76 (both figured).

TYPE LOCALITY AND HORIZON. R. Clydach, Nr. Gilwern, Lower Z Zone. Sample ZLA 27.

RANGE. North Crop ZL 3–ZLA 27, Avon Gorge K 17.

DESCRIPTION. The unit is asymmetrical, the blade always being on the right when viewed from the posterior. The blade is low, consisting of 4 or 5 denticles all of approximately equal height, the tallest denticle being either the posterior or the

penultimate posterior. The platform is ornamented by two rows of irregular nodes. The margins are separated by a shallow trough, which generally tends to close towards the anterior, and occasionally possess a short carina at the posterior extremity. The lateral denticles on the blade side of the platform tend to be rather larger than those on the other side. In smaller specimens, the basally confluent platform denticles have sharply pointed, discrete apices in lateral view, but they become more blunt in larger specimens. The platform walls are deep, and the aboral outline is straight over the anterior two-thirds, but the posterior one-third can be deflected downwards, especially in smaller specimens.

In aboral view, the unit is excavated, the cavity being large, flaring and asymmetrical, extending from nearly the posterior extremity of the platform to its junction with the anterior blade.

REMARKS. This species can be distinguished from all other clydagnathids by the character of the blade.

Clydagnathus gilwernensis sp. nov.

Plate 2, fig. 1a-d

DERIVATION OF NAME. From the locality at Gilwern.

DIAGNOSIS. Clydagnathid with short, high, medial, anterior blade, and short posterior carina occasionally developed into a short posterior blade.

MATERIAL. 7 specimens : Holotype X 78 (figured).

TYPE LOCALITY AND HORIZON. R. Clydach, Nr. Gilwern, K Zone. North Crop. Sample KL 1.

RANGE. North Crop KL 1-KL 6, Avon Gorge K 6.

DESCRIPTION. The anterior blade is short and situated medially. It commonly bears three denticles, the posteriormost being the tallest and most massive. The blade denticles, which have blunt or chevron tips, are laterally compressed, and are fused at their bases. They decrease rapidly in size anteriorly. The antero-aboral portion of the blade is strongly protruding and bluntly spatulate in profile. The platform is long, slender and posteriorly sharply pointed ; it has two lateral rows of blunt, triangular lateral nodes, with a shallow medial trough which is filled at the posteriormost extremity by a short carina of 2 to 4 nodes, which may extend beyond the platform to give a short posterior blade. On some specimens the carina may be absent.

In lateral view the posterior platform of young forms is "upstepped" relative to the blade, but in mature specimens the unit is arched about the cavity.

In aboral view there is an asymmetrical medial cavity situated in the anterior third of the platform. It has longitudinally thickened lips ; a faint groove sometimes runs a short distance either side of the cavity.

REMARKS. In gross morphological terms *C. gilwernensis* is similar to *Patrognathus variabilis* but the vastly different cavity, the distinctive blade and excavated medial trough serve to distinguish it. It would appear that the two forms were the result

of convergent evolution, since the ancestors of *C. gilwernensis* were of spathognathodid stock. They may have been functionally similar.

Clydagnathus unicornis sp. nov.

Plate 2, figs. 2a-3d, 5a, b

DERIVATION OF NAME. From the single large denticle on the blade.

DIAGNOSIS. Clydagnathid with restricted anterior lateral blade, consisting essentially of one large denticle; median trough opens anteriorly; basal cavity elongated and symmetrical.

MATERIAL. 25 specimens: Holotype X 79, Paratypes X 80, X 81 (all figured).

TYPE LOCALITY AND HORIZON. R. Clydach, Nr. Gilwern, Lower Z Zone. North Crop. Sample Z 2A.

RANGE. North Crop ZL 4-ZLA 27, Avon Gorge Z 1.

DESCRIPTION. The unit is asymmetrical, the blade always occurring on the right side viewed from the posterior, and consisting essentially of one large denticle, subtriangular in shape and posteriorly inclined. The tip of the denticle is sharply pointed and the anterior edge convex, forming a continuous curve with the spatulate antero-aboral margin of the blade. The anterior face of this denticle occasionally bears 2 or 3 small denticles which are fused with it, so that only thin blunt apices are visible.

The platform is uneven, consisting of two rows of low irregular marginal nodes, separated by a very shallow, but rather wide, medial trough. A short carina may sometimes be present in the posterior extremity. The platform walls are deep, and on the basal faces are disrupted by the flaring of the lips of the basal cavity. In lateral view, the marginal nodes are sharply pointed in smaller specimens, but blunt or flat in larger specimens.

In aboral view the unit is excavated, the cavity being asymmetrical, expanded more on the inner side than the outer. The cavity runs posteriorly, becoming narrower and shallower towards the posterior termination. It is grooved along its whole length.

REMARKS. This species probably arose from *Clydagnathus cavusformis* by fusion of the anteriormost blade denticles to give an essentially unidenticate blade, and by the elongation of the cavity, rather than the laterally expanded cavity of *C. cavusformis*.

Clydagnathus sp. nov. A

Plate 2, figs. 4a-d

MATERIAL. 2 specimens: figured, X 82.

RANGE. North Crop KL 7-KL 13.

DESCRIPTION. A clydagnathid with a high, equally tridenticulate anterior blade, a short posterior blade, and a heavy asymmetrical basal cavity.

The unit is arched and triangular in cross-section. The blade is short and high, consisting of three equal denticles fused into a blade but with free tips which are slightly divergent. The platform is lanceolate, nearly four times as long as wide, and is ornamented with two rows of denticles along the platform margins, separated by a straight, shallow, smooth trough. The denticles tend to be transversely elongate. The posterior part of the platform possesses a short carina, of about three nodes, which is produced posteriorly to give a short posterior blade.

In lateral view the platform posterior to the basal cavity is deflected continuously downwards through 30° , and its depth decreases markedly towards the posterior. The basal cavity is large, ovate, nearly symmetrical and is confined to the anterior part of the platform ; it flares slightly in lateral view.

REMARKS. This clydagnathid is similar to *C. darensis*, but the blade is much higher, has fewer denticles and the deflected posterior platform is unique. The cavity is also different in that all other clydagnathids have an obviously asymmetrical cavity, whereas this form possesses a nearly symmetrical cavity.

Genus *EUPRIONIODINA* Ulrich & Bassler 1926

1925 *Euprioniodina* Bassler : 219. (nom. nud.)

1925 *Synprioniodina* Bassler : 219. (nom. nud.)

1926 *Euprioniodina* Ulrich & Bassler : 29.

1926 *Synprioniodina* Ulrich & Bassler : 42.

TYPE SPECIES. *Euprioniodina deflecta* Ulrich and Bassler 1926.

DESCRIPTION. This genus is characterized by its general pick-shape, with a short, denticulated, highly compressed anticusp. The posterior limb is long and bears numerous erect denticles.

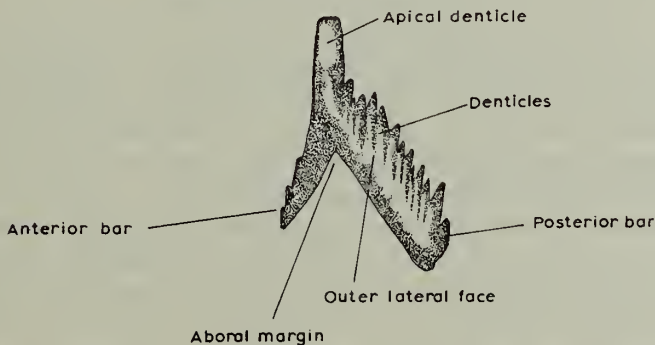


FIG. 21. *Euprioniodina* sp. showing morphological terms used in the text.

REMARKS. The genera *Synprioniodina*, *Euprioniodina* and *Neoprioniodus* have essentially the same outline and differ in the presence, or absence, of denticles on the antiscusp. The genera *Synprioniodina* and *Euprioniodina* are here considered synonyms and are characterized by a denticulated antiscusp. *Neoprioniodus* is a similar pick-shaped form to *Euprioniodina*, but has no denticulated antiscusp.

As Scott and Collinson (1961) pointed out, there appears to be a number of forms intermediate between *Euprioniodina* and *Neoprioniodus*. Sannemann (1955), Bischoff (1956) and Helms (1959) have assigned all such specimens to the genus *Prioniodina*. However, the specimens they refer to *Prioniodina* do not closely resemble the type species of *Prioniodina*, *Prioniodina subcurvata*. A detailed revision of the pick-shaped forms is necessary, but as few specimens referable to the genus *Euprioniodina* have been found in the present faunas, it is impossible to undertake this study.

It is difficult to distinguish *Euprioniodina* from some species of *Apatognathus*. We have divided the two genera by assigning to *Apatognathus* those species in which there is conspicuous lateral flexing of one or both bars.

Euprioniodina caverna (Collinson & Druce)

Plate 22, figs. 11a, b

Synprioniodina caverna Collinson & Druce in press.

MATERIAL. 14 specimens : figured, X 83.

RANGE. North Crop 3D 14/15.

DESCRIPTION. The present specimens have a greatly elongated anterior bar, which is more or less straight, and which bears a series of at least twelve laterally compressed, confluent denticles on its anterior edge. These are small and of uniform size, being considerably smaller than any of those on the posterior bar. The apical denticle, which is aligned with the main line of the anterior bar, is relatively short ; it is sharply pointed, with sharp anterior edges and a gently convex outer lateral face. The junction of the anterior and posterior bars is marked by the development of an apical lamella, which is depressed and has a flat surface in outer lateral view. The posterior bar is straight to feebly convex in outer lateral view and is also flexed inwardly. It bears a series of about 14 denticles on its oral edge, which show a broad tendency to increase in size posteriorly, though this is not a regular feature. They are basally confluent but apically discrete and are elongated and pointed, being at least two to three times as long as those of the anterior bar. They are directed forward parallel to the apical denticle and are also curved gently inward.

In inner lateral view the surface of the posterior bar is gently convex, and that of the anterior bar more or less flat. The denticles are distinctly curved inward and there is a very sharp aboral flexure below the apical denticle with an angular to strongly convex apical lamella.

The aboral surface is excavated by a narrow groove along the whole of its length, this being a continuation of the wide flaring cavity below the apical lamella.

Euprioniodina microdenta (Ellison)

Plate 22, figs. 16a, b

- 1933 *Synprioniodina* sp. Gunnell : 269, Pl. 31, fig. 6.
 1941 *Synprioniodina microdenta* Ellison : 108-111, 119, Pl. 20, figs. 43-46.
 1941 *Synprioniodina microdenta* Ellison ; Ellison & Graves : 3-4, Pl. 1, fig. 10.
 1944 *Synprioniodina microdenta* Ellison ; Branson : 327.
 1952 *Synprioniodina microdenta* Ellison ; Rhodes : 893, Pl. 126, fig. 4.

MATERIAL. 2 specimens : figured, X 84.

RANGE. North Crop 3D 4-3D 14/15.

DESCRIPTION. The present specimens are characterized by a very short anterior bar and a greatly elongated posterior bar. In outer lateral view the posterior bar is greatly elongated, tending to increase in depth posteriorly. Its outer lateral face is flat to gently convex, and it is about equal in depth to the length of the free denticles. Its oral surface bears about 14 long, slender denticles, more or less subcircular in cross-section, though showing a slight tendency to lateral flattening. They are discrete for most of their length and are sharply pointed. They are separated by very much finer needle-like denticles, which are only a quarter to a third the width of those of the major series. All denticles slope anteriorly, and are also more or less curved inwards. They tend to increase in size towards the posterior third of the bar. The outer lateral face of the main cusp is gently convex and it has conspicuously sharp anterior and posterior edges. The anterior bar is very short, being only about one-sixth the length of the posterior ; it tapers rapidly towards its distal end. It bears 3 or 4 minute denticles, which lie parallel to the main cusp. In inner view the whole unit is gently flexed, so that the inner lateral faces are very feebly concave. The aboral margin of the posterior bar is more or less straight in lateral view, apart from its rapid curvature below the apical denticle. The two bars diverge at an angle of about 60°. The apical denticle is about three times the width of the largest denticles of the posterior bar.

Euprioniodina sp. nov. A

Plate 22, figs. 13a, b

MATERIAL. 1 specimen : Holotype X 86 (figured).

LOCALITY AND HORIZON. Hosie Limestone, Fife Coalfield. Sample HOSIE 2B.

RANGE. Scotland HOSIE 2B.

DESCRIPTION. A *Euprioniodina* with a massive, laterally compressed, incurved and recurved apical denticle. The anterior bar is short and pointed with up to three confluent denticles. The posterior bar is short with three minute denticles developed on the posterior edge of the apical denticle.

The present specimen is very fragmentary, but it shows a massive apical denticle which is laterally compressed with sharp anterior edges and gently convex lateral faces. It is recurved sharply posteriorly in its lower portion. The short anterior bar is pointed and bears a series of two or three confluent denticles on its oral edge

which tend to decrease in size anteriorly. Three very small, confluent, laterally compressed denticles are developed on the posterior edge of the apical denticle. These are of minute size. The anterior aboral lateral face of the apical denticle is very strongly expanded laterally, whereas that of the outer lateral face is flat to feebly convex. The posterior bar is shallow and strongly laterally compressed, its outer lateral face being flat and its inner very feebly convex. The apical denticle is incurved as well as recurved.

Euprioniodina sp.

Plate 22, figs. 15a, b

MATERIAL. 16 specimens : figured, X 85.

RANGE. Avon Gorge K 4-K₂ 1.

DESCRIPTION. The apical denticle is relatively short and compressed, with a denticulate anticusp equal in length to the apical denticle. The apical denticle is strongly compressed laterally, with sharp anterior and posterior edges. The anticusp is a continuation of the main denticle and both are slightly concave inward. The anticusp bears up to 5 laterally compressed denticles, the anterior margins of which are subparallel to the apical denticle. The posterior limb is long and thin, and is sharply bowed immediately posterior to the apical denticle, with little additional bowing behind this. The entire unit is sharply arched. The posterior limb is straight and bears at least 14 confluent, sub-equal, sub-rounded to laterally compressed denticles. The minute pit is located at the base of the cusp and has slightly flared lateral lips. The pit is deep, with a sharp point extending into the base of the apical denticle.

Genus *GENICULATUS* Hass 1953

1953 *Geniculatus* Hass : 77.

TYPE SPECIES. *Polygnathus* ? *claviger* Roundy 1926.

Geniculatus sp.

Plate 31, fig. 24

MATERIAL. 2 specimens : figured X 327.

RANGE. Scotland DUN 59.

DESCRIPTION. Two broken specimens are present in one sample from Dunbar. Both specimens are anterior bars which are greatly inflated and bear a series of laterally compressed fused denticles with free chevron tips. In aboral view the bar is broad and has a fine median groove.

REMARKS. The inflated bar enables the present specimens, although broken, to be referred to *Geniculatus*.

Genus *GNATHODUS* Pander 18561856 *Gnathodus* Pander : 33.TYPE SPECIES. *Gnathodus mosquensis* Pander 1856.*Gnathodus antetexanus* Rexroad & Scott

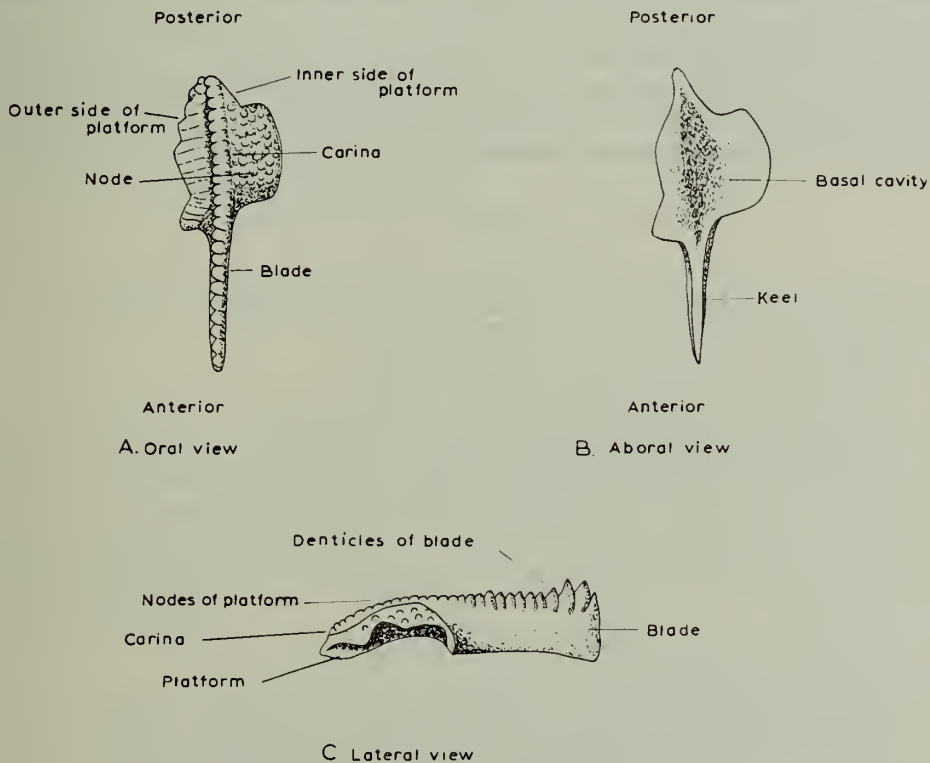
Plate 18, figs. 6a-c, 8a, b, 13a-d

1947 *Gnathodus texanus* Roundy ; Mehl & Thomas : 10, Pl. 1, fig. 3.1957 *Gnathodus texanus* Roundy ; Bischoff (*partim*) : 25, Pl. 3, fig. 22 only.1959 *Gnathodus texanus* Roundy ; Voges (*partim*) : 284, Pl. 33, figs. 40, 42 only.1962 *Gnathodus* n. sp. aff. *Gnathodus texanus* Roundy ; Collinson, Scott & Rexroad : chart 3.1964 *Gnathodus antetexanus* Rexroad & Scott : 28, Pl. 2, figs. 7-10.

MATERIAL. 10 specimens : figured, X 412, X 413, X 414.

RANGE. North Crop ZLA 32-ZLA 33, Avon Gorge Z 33-C 9.

DESCRIPTION. Most of our specimens are broken, but the platforms are preserved. They show the typical narrow outer platform, with a sparse covering of nodes, and the broader inner platform with the large upstanding node, which are characteristic

FIG. 22. *Gnathodus* sp. showing morphological terms used in the text.

features of the species. They are very similar to the specimens illustrated by Rexroad and Scott.

***Gnathodus avonensis* sp. nov.**

Plate 18, figs. 9a-d

DERIVATION OF NAME. After the type section in the Avon Gorge.

DIAGNOSIS. *Gnathodus avonensis* sp. nov. is closely similar to *Gnathodus simplicatus* sp. nov. but bears a node on one side of upper surface of platform.

MATERIAL. 2 specimens : Holotype X 411 (figured).

TYPE LOCALITY AND HORIZON. Avon Gorge Z₂ Limestone. Sample Z 38.

RANGE. Avon Gorge Z 38.

DESCRIPTION. The platform is confined to the posterior third of the unit and is unornamented except for the presence of a single node on one side of the platform. It is biconvex in outline and narrow. In lateral view the blade is rather rectangular in outline, the 10 or more denticles being of uniform size. The anterior edge is straight, and forms a right angle with the aboral edge of the blade, which may be slightly curved. The oral edge is straight in the anterior half of the unit and slightly arched in the posterior half of the unit. The platform has a concave aboral margin in lateral view, and is less deep than the blade. There is a flaring and elongate basal cavity below the platform.

REMARKS. *Gnathodus avonensis* sp. nov. developed from *G. simplicatus* sp. nov. by the formation of a single node on the side of the platform. *G. avonensis* sp. nov. is a homoeomorph of *G. nodosus* Bischoff.

***Gnathodus bilineatus* (Roundy)**

Plate 18, figs. 14a-17d

- 1900 *Polygnathus* (*Gnathodus*) *Mosquensis* Pander (sic) Hinde : 342, Pl. 9, figs. 2-4.
 1926 *Polygnathus bilineatus* Roundy : 13, Pl. 3, figs. 10a-c.
 1926 *Polygnathus texanus* Roundy : 14, Pl. 3, figs. 13a, b.
 1928 *Gnathodus mosquensis* (Pander) Holmes : 6, fig. 31.
 1939 *non Gnathodus bilineatus* Cooper : 388, Pl. 42, figs. 59-60.
 1941 *Gnathodus pustulosus* Branson & Mehl : 172, Pl. 5, figs. 32-39.
 1953 *Gnathodus bilineatus* (Roundy) Hass : 78, Pl. 14, figs. 25-29.
 1956 *Gnathodus bilineatus* (Roundy) Elias : 118, Pl. 3, figs. 23-29.
 1956 *Gnathodus pustulosus* (Branson & Mehl) Elias : 115, Pl. 3, figs. 1-8.
 1957 *Gnathodus bilineatus bilineatus* (Roundy) Bischoff : 21, Pl. 3, figs. 11, 15-20 ; Pl. 4, fig. 1.
 1957 *Gnathodus bilineatus bilineatus* (Roundy) Ziegler in Flügel & Ziegler : 38, Pl. 3, figs. 1, 2 only.
 1957 *Gnathodus modocensis* Rexroad : 30, 31, Pl. 1, figs. 15-17.
 1958 *Gnathodus modocensis* Rexroad ; Rexroad : 17, 18, Pl. 1, figs. 1, 2.
 1959 *Gnathodus bilineatus* (Roundy) Voges : 282, Pl. 33, figs. 28-30.
 1959 *Gnathodus* (*Harltonodus*) *bilineatus* (Roundy) Elias : 145, Pl. 1, figs. 3-12.
 1959 *Gnathodus* (*Harltonodus*) *bransonii* Elias : 147, Pl. 1, figs. 13-18.
 1959 *Gnathodus* (*Harltonodus*) *minutus* Elias : 148, Pl. 1, figs. 22-25.
 1959 *Gnathodus* (*Harltonodus*) *multilineatus* Elias : 149, Pl. 1, figs. 26-28.

- 1960 *Gnathodus smithi* Clarke : 26, Pl. 4, figs. 13-14 ; Pl. 5, figs. 9 & 10.
 1961 *Gnathodus bilineatus* (Roundy) Higgins : Pl. 10, fig. 5.
 1962 *Gnathodus bilineatus* (Roundy) Higgins : (*partim*), Pl. 2, fig. 25 only.
 1962 *Gnathodus bilineatus bilineatus* (Roundy) Meischner : 31, fig. 10.
 1965 *Gnathodus bilineatus* (Roundy) Dunn : 1148, Pl. 140, figs. 7-9.
Gnathodus bilineatus (Roundy) Collinson & Druce in press.

MATERIAL. 765 specimens, North Crop : figured X 416, X 417, X 93, X 94.

RANGE. North Crop 3D 10-3D 23.

DESCRIPTION. This is one of the most abundant species in the higher parts of the section of the North Crop and, although it displays considerable variation, its main features agree closely with those described by earlier authors, especially Hass (1953) and Bischoff (1957). There is considerable variation in the ontogeny of this species. The main variation concerns the increase in the relative size and angularity of outline of the outer lateral platform, and its increasingly strongly developed ornamentation. In young forms this tends to be inconspicuously nodose and rather irregular, but in older forms it becomes either longitudinally linear or broadly concentric in disposition, and the nodes become stronger, tending to form elongate ridges. There is also considerable variation in the strength of the inner lateral platform and of the transverse denticles developed upon it. In numbers of specimens it is pinched inwards in the anterior half when seen in oral view. There is also appreciable variation in the depth and relative width of the sulcus that separates these denticles from the carina. In spite of its extent, the variation appears to be continuous, and there is no obvious difference between specimens collected from different parts of the range of the species.

Gnathodus commutatus (Branson & Mehl)

Plate 19, figs. 9a-12d

- 1941 *Spathognathodus commutatus* Branson & Mehl : 98, Pl. 19, figs. 1-4.
 1941 *Spathognathodus commutatus* Branson & Mehl ; Ellison & Graves : 3, 4. Pl. 2, fig. 6, (*non* Pl. 2, fig. 4=*Gnathodus symmutatus*?).
 1953 *Gnathodus inornatus* Hass : 80, Pl. 14, figs. 9-11.
 1956 *Spathognathodus commutatus* Branson & Mehl ; Elias : 119, Pl. 3, figs. 19-22.
 1956 *Spathognathodus inornatus* Hass ; Elias : 119, Pl. 3, figs. 37-39.
 1956 *Spathognathodus* cf. *inornatus* Elias : 119, Pl. 3, figs. 41, 42, (*non* Pl. 3, figs. 62, 63=*G. symmutatus*?).
 1957 *Gnathodus commutatus commutatus* (Branson & Mehl) Bischoff : 22, Pl. 4, figs. 2-6, 15.
 1957 *Spathognathodus* cf. *S. commutatus* Branson & Mehl ; Rexroad : 38, Pl. 3, figs. 23, 24.
 ? 1957 *Gnathodus commutatus commutatus* (Branson & Mehl) Ziegler in Flugel & Ziegler 39, Pl. 3, fig. 21.
 1958 *Gnathodus inornatus* Hass ; Stanley : 465, Pl. 68, figs. 5, 6.
 1958 *Spathognathodus* cf. *S. commutatus* Branson & Mehl ; Rexroad : 26, Pl. 6, fig. 8.

- non 1958 *Gnathodus commutatus commutatus* (Branson & Mehl) Lys & Serre : 891, Pl. 9, figs. 2a, b (= *G. symmutatus*).
- 1959 *Gnathodus commutatus commutatus* (Branson & Mehl) Voges : 281.
- 1960 *Spathognathodus commutatus* Branson & Mehl ; Clarke : 19, Pl. 3, figs. 4, 5.
- 1960 *Gnathodus commutatus commutatus* (Branson & Mehl) Serre & Lys : 39, fig. 3.
- 1961 *Gnathodus commutatus* (Branson & Mehl) Rexroad & Burton : 1153, Pl. 139, figs. 1-3.
- 1961 *Gnathodus commutatus* var. *commutatus* (Branson & Mehl) Higgins : 212, Pl. 10, figs. 6, text-fig. 1a, (left figure only).
- 1962 *Gnathodus commutatus commutatus* (Branson & Mehl) Higgins : Pl. 2, fig. 22.
- 1962 *Gnathodus commutatus commutatus* (Branson & Mehl) Meischner : 31, text-fig. 10.
- 1963 *Gnathodus commutatus commutatus* (Branson & Mehl) Bouckaert & Higgins : 17, fig. 3.
- 1964 *Gnathodus commutatus pellaensis* Rexroad & Furnish : 671, Pl. 111, fig. 3.
Gnathodus commutatus (Branson & Mehl) Collinson & Druce in press.

MATERIAL. 425 specimens : figured, X 418, X 95, X 96, X 97.

RANGE. North Crop CYD 7-3D 22, Avon Gorge S 53.

DESCRIPTION. This species has recently been redefined by Collinson & Druce (in press) and it is their revised description which is accepted here. Although the species, which is represented by many specimens in the present collections, shows appreciable variation, the distinctive characteristics are the regular sub-rectangular outline of the blade when seen in lateral view, the regular height and thickness of the confluent denticles which make up the blade, the rather square anterior profile of the blade, and the small posteriorly restricted sub-oval to sub-circular unornamented platform. This platform is always asymmetrical in detail, and shows considerable variation in its basal outline and in the degree of flexure of its basal margin. This variation is so obviously transitional, however, that it seems impossible to distinguish any discrete categories on the basis of it. The chief variation is in the general form of the posterior platform, which varies from slenderly sub-elliptical to sub-circular, in the degree of symmetry of the posterior platform, which is generally marked by the inner margin being wider anteriorly than it is posteriorly, and in the relation of the carina to the posterior margin of the platform. In some cases the posterior margin of the platform tends to be relatively elongated, while in others it tends to be bluntly rounded. The carina may, in some specimens, extend slightly beyond the posterior margin when seen in oral view (Pl. 19, fig. 9d) but in others it terminates anteriorly to the margin. In a few cases the posterior portion of the carina is strongly deflected laterally. In most individuals the central blade tends to become thicker posteriorly, where it forms the carina of the posterior platform (e.g. Pl. 19, fig. 10d). The surface of the posterior platform is smooth and the platform itself occupies only the posterior quarter or third of the total length of the unit. The broad variation within this species noted by Collinson and Druce is also shown by the present specimens.

REMARKS. In many specimens the blade is straight, but in others it is gently curved in a horizontal plane ; in these cases the wider of the two platforms in the anterior position is always that on the concave side of the blade.

Gnathodus cuneiformis Mehl & Thomas

Plate 8, figs. 6a-c

- 1939 *Gnathodus mosquensis* Pander ; Cooper (*partim*) : 388, Pl. 41, figs. 23-25 only ; Pl. 42, figs. 75, 76.
 1939 *Gnathodus stinus* Cooper : 388, Pl. 14, figs. 40, 41.
 1947 *Gnathodus cuneiformis* Mehl & Thomas : 10, Pl. 1, fig. 2.
 1962 *Gnathodus cuneiformis* Mehl & Thomas ; Collinson Scott & Rexroad : Chart 3, p. 10, 22, 23.

MATERIAL. I specimen : figured, X 98.

RANGE. Avon Gorge S II.

DESCRIPTION. This species is characterized by a high, slightly asymmetrical, arrow-shaped platform, bearing a single row of nodes on either side of the carina. The flanks of the platform are smooth and steep.

REMARKS. The shape of the platform and the single row of nodes on either side of the carina distinguish this species from other gnathodids. In North America this species is characteristic of the Sedalia, Fern Glen and Burlington Formations.

Gnathodus delicatus Branson & Mehl 1938

Plate 18, figs. 12a-d. Plate 30, figs. 6a-c

- 1938 *Gnathodus delicatus* Branson & Mehl : 145, Pl. 34, figs. 25-27.
 1938 *Gnathodus perplexus* Branson & Mehl : 145, Pl. 45, fig. 24.
 1939 *Gnathodus texanus* (Roundy) Cooper : 388, Pl. 41, figs. 26, 27.
 1951 *Gnathodus delicatus* Branson & Mehl ; Hass : 394, Pl. 46, figs. 3-7.
 1957 *Gnathodus commutatus punctatus* Bischoff ; Flügel & Ziegler : Pl. 111, figs. 16, 17, 24.
 1959 *Gnathodus delicatus* Branson & Mehl ; Voges : 283, Pl. 33, figs. 31-33.
 1960 *Gnathodus delicatus* Branson & Mehl ; Kronberg, Pilger, Scherp & Ziegler : Pl. 4, figs. 7-12.
 1962 *Gnathodus delicatus* Branson & Mehl ; Collinson, Scott & Rexroad : 10, Chart 3, 21, 22.
 1962 *Gnathodus delicatus* Branson & Mehl ; Higgins : 13, Pl. 3, fig. 33 ; Pl. 2, figs. 23, 24.
 1962 *Gnathodus delicatus* Branson & Mehl ; Ziegler : Pl. 4, fig. 4.
 1963 *Gnathodus delicatus* Branson & Mehl ; Ziegler : 327, Pl. 2, figs. 5, 7, 8, 9, 13, 14.
 1963 *Gnathodus delicatus cuneiformis* Ziegler : Pl. 2, fig. 12.
 1964 *Gnathodus delicatus* Branson & Mehl ; Rexroad & Scott : 29-30, Pl. 2, figs. 4-6.
 1964 *Gnathodus delicatus* Branson & Mehl ; Higgins, Wagner-Gentis & Wagner : 226, Pl. V, fig. 24.
 1964 *Gnathodus* cf. *delicatus* Branson & Mehl ; Higgins, Wagner-Gentis & Wagner : 226, Pl. V, fig. 23.

MATERIAL. 11 specimens : figured, X 87, X 426.

RANGE. North Crop ZLA 5-ZLA 6, Avon Gorge Z 28-Z 37.

DESCRIPTION. The asymmetrical platform of this species is ornamented by two rows of nodes, one on the narrower inner side, and one on the wider outer side, both running parallel to the carina. The inner platform bears a row of up to 9 denticles parallel to the carina, and slopes steeply at its margin. The outer platform bears a row of 5 denticles, parallel to the carina, on its inner side, and may also show traces of

the development of a second row. There is a uniform sharp slope towards the margin. The platform is arrow-shaped, being widest at the anterior. It becomes pointed towards the posterior. The inner platform extends further anteriorly than does the outer. The denticulate blade is equal in length to the platform. In lateral view, the oral and aboral edges of the blade are straight; the oral and aboral edges of the platform are slightly curved. The anterior and posterior edges are straight.

REMARKS. Specimens from the Z₂ beds of the Avon Gorge have a row of nodes on either side of the carina. In some examples, the anterior nodes of the inner side of the platform are fused to form a parapet. These forms are considered to be transitional with *Gnathodus semiglaber*, or possibly with *Gnathodus antetexanus*.

This species is common in conodont faunas of late Kinderhookian and early Valmeyerian age in North America. Rexroad & Scott (1964) after studying hundreds of specimens, came to the conclusion that the low, broad, asymmetrical outline of the platform, and the linear arrangement of nodes seem to be consistent characters, and similar specimens obtained in the present study have, therefore, been placed in this species.

Gnathodus girtyi girtyi Hass

Plate 17, figs. 9a-12d

- 1953 *Gnathodus girtyi* Hass : 80, Pl. 14, figs. 22-24.
 1956 *Gnathodus girtyi* Hass ; Elias : 118, Pl. 3, figs. 30, 31.
 1957 *Gnathodus girtyi* Hass ; Bischoff (*partim*) : 24-25, Pl. 4, figs. 16-17, 22-23 (*non* Pl. 4, fig. 21=*Gnathodus girtyi simplex* Dunn).
 1957 *Gnathodus girtyi* Hass : Lys & Serre : 1043, Pl. 2, figs. 7a-c.
 1958 *Gnathodus* ? sp. Rexroad : 18, Pl. 1, figs. 3-5.
 1960 *Gnathodus clavatus* Clarke : 28, Pl. 4, figs. 4-6 (*non* Pl. 4, figs. 7-9=*G. girtyi simplex* Dunn).
 1961 *Gnathodus girtyi* Hass ; Higgins : 220, Pl. 10, fig. 4.
 1961 *Gnathodus* n. sp. Rexroad & Collinson : Pl. 1.
 1961 *Gnathodus girtyi* Hass ; Rexroad & Jarrell : 2015.
 1962 *Gnathodus girtyi* Hass ; Collinson, Scott & Rexroad : Chart 4.
 1962 *Gnathodus girtyi* Hass Form A Meischner : 31, text-fig. 10.
 1963 *Gnathodus girtyi* Hass Form C Bouckaert & Higgins : 17, text-fig. 3.
Gnathodus girtyi girtyi Hass ; Collinson & Druce in press.

MATERIAL. 780 specimens : figured, X 103, X 104, X 105, X 106.

RANGE. North Crop CYD 5-3D 23, Avon Gorge D 26.

DESCRIPTION. The main features of this subspecies have been described in detail by Collinson & Druce (in press) and the present specimens, although showing some variation, agree in all major respects with their description. The most distinctive features are the long slender form of the unit, with the anterior blade commonly being strongly laterally compressed and relatively high in relation to its length; it occupies at least half the total length of the unit. It is straight to curved in oral view. The unit as a whole is straight or curved in a horizontal plane, and the curvature is chiefly concentrated in the posterior portion of the carina (e.g. Pl. 17,

figs. 11, 12). The blade is generally highest at its anterior end, although the two most anterior denticles may be relatively small ; the posterior end of the unit tends to be lower. The blade has a bluntly spatulate to rectangular anterior end and a more or less straight or very feebly convex aboral edge. The denticles are fused to about mid-height but their apices are discrete.

The carina consists of low, fused denticles, of about equal height to those at the posterior portion of the anterior blade. The carina is depressed in the posterior half of the platform, and the level of the denticles tends to be relatively higher than those of the lateral ornament, which reaches about two thirds of the total depth of the posterior platform from the top of the carina. The posterior platform itself is characterized by a variably asymmetrical basal outline. In some specimens the basal outline is almost biconvex, but in most the outer aboral margin is more conspicuously flared than the inner ; in a few individuals it is so strongly flared that it gives to the basal outline a form reminiscent of such species as *G. bilineatus* or *G. semiglaber* (e.g. Pl. 17, fig. 12a). In spite of this, the platform ornament remains distinctive ; the ornament on the inner lateral surface of the platform extends further forward than that on the outer, and consists of a low series of fused nodes, running sub-parallel to the carina but converging with it in the posterior platform, and looping round the posterior end of the carina to give a bluntly rounded, pointed outline (e.g. cf. Pl. 17, figs. 11b, 12b). The outer platform ornament tends to be less conspicuous than that of the inner ; the lateral ridges, which characterize the denticles of the inner platform, are absent from the outer platform.

The basal cavity is flaring and asymmetrical, being deepest in the anterior third of the platform and continuing for a variable distance below the posterior portion of the anterior blade.

REMARKS. In some individuals (e.g. Pl 17, fig. 10b) the posterior carina tends to continue somewhat beyond the level of the lateral denticles, which then tend to merge with it anterior to the termination of the platform. In this they approach other subspecies of the genus but are otherwise distinguishable from them.

Gnathodus girtyi collinsoni subsp. nov.

Plate 16, figs. 5a-8d

1962 *Gnathodus girtyi* Form C Meischner : 31, fig. 10.

1963 *Gnathodus girtyi* B Hass ; Bouckaert & Higgins : 17.

1965 *Gnathodus roundyi* Gunnell ; Murray & Chronic (*partim*) : 598, Pl. 71, figs. 5, 6 only.

DERIVATION OF NAME. After Dr. Charles W. Collinson.

DIAGNOSIS. Subspecies of *Gnathodus girtyi* in which lateral denticulation of platform is confined to inner lateral side. Very feeble nodes may sometimes be developed on outer lateral platform.

MATERIAL. 13 specimens : Holotype X 99, Paratypes X 100, X 101, X 102 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample 3D 14/15.

RANGE. North Crop 3D 8-3D 14/15.

DESCRIPTION. In broad morphology this subspecies resembles *Gnathodus girtyi girtyi*. The form of the anterior blade, and its general denticulation, the general outline and the size and depth of the posterior platform are generally similar. The number of denticles in the main blade (including the carina) ranges from 21 to 25.

The distinctive feature of this subspecies is the denticulation of the posterior platform. The inner-lateral oral surface of the platform has a conspicuously developed, parapet-like series of denticles, those at the anterior end being higher than those at the posterior. These denticles are individually rather small and inconspicuous, but the ridge which they form is itself made conspicuous by the general height and thickness of the base. They number about 9, and are small rounded discrete node-like structures. Those at the anterior end of the series are separated from the carina by a shallow longitudinal groove. Towards the posterior end of the series the denticles converge with the main carina, which they meet near the anterior end of the fourth denticle from the posterior terminus of the unit. In lateral view these denticles form a conspicuous shoulder-like feature of the platform. The sloping anterior aboral margin terminates near the anterior end of the basal cavity. On the outer lateral platform, very indistinct node-like denticles may sometimes be developed but they are always a relatively inconspicuous feature, though in a very few specimens they are barely discernible in both lateral and oral view (e.g. Pl. 16, figs. 7a-d).

Gnathodus girtyi simplex Dunn

Plate 16, figs. 1a-4d

- 1957 *Gnathodus girtyi* Hass ; Bischoff : 24, 25, Pl. 4, fig. 21 (non Pl. 4, figs. 16, 17, 22, 23=*G. girtyi girtyi* Hass ; non Pl. 4, figs. 18-20=*G. girtyi turritus* Collinson & Druce.
 1957 *Gnathodus girtyi* Hass ; Ziegler in Flügel & Ziegler : 40-41, Pl. 3, figs. 6, 9-13, 20.,
 1957 *Gnathodus bilineatus semiglaber* Bischoff ; Ziegler in Flügel & Ziegler : Pl. 3, fig. 22 (non Pl. 3, figs. 5, 8, 14, 23=*Gnathodus semiglaber*).
 1959 *Gnathodus texanus* Roundy ; Voges : 284-285, Pl. 33, figs. 40-43.
 1960 *Gnathodus clavatus* Clarke (*partim*) : Pl. 4, figs. 7-9 (non pl. 4, figs. 4-6=*Gnathodus girtyi girtyi* Hass).
 1962 *Gnathodus texanus* Roundy ; Higgins : Pl. 3, fig. 28.
 1962 *Gnathodus girtyi* Form B Meischner : 31, text-fig. 10.
 1963 *Gnathodus girtyi* Form A Hass ; Bouckaert & Higgins : 17, text-fig. 3.
 1965 *Gnathodus girtyi simplex* Dunn : 1148, Pl. 140, figs. 2, 3, 12.
Gnathodus girtyi simplex Dunn ; Collinson & Druce in press.

DIAGNOSIS. Subspecies of *G. girtyi* in which lateral denticles on both inner and outer lateral margins of platform are more feebly developed than in *G. girtyi girtyi* and are also restricted to anterior and medial parts of platform.

MATERIAL. 260 specimens : figured, X 107, X 108, 110, 111.

RANGE. North Crop CYD 7A-3D 23, Avon Gorge D 26.

DESCRIPTION. In lateral and aboral views the main features of this subspecies are closely similar to those of *G. girtyi girtyi* especially in the form of the anterior blade

and of the basal cavity. The most conspicuous difference is in the character of the accessory lateral denticles on the posterior platform. The denticles on the inner lateral platform are relatively more strongly developed than those on the outer. They consist of up to 9 denticles, the highest and most massive being at the anterior end, and are separated by a trough from the main median carina. Those towards the posterior end of the series tend to be smaller and also to be developed nearer to the carina. The denticles of the outer lateral platform are smaller and fewer in number and extend further posteriorly than those on the inner lateral platform. In oral view both series of lateral nodes converge posteriorly and fuse with the median carina, the carina extending further posteriorly than either series of lateral denticles. In lateral view the denticles of the inner series approach the height of those on the median carina, but are still fractionally shorter. In outer lateral view the denticles at the posterior end of the outer lateral series tend to be slightly larger and more conspicuous than those at the anterior end. The apron on the outer lateral platform, when seen in oral view, is relatively much more laterally expanded than that of the inner lateral platform. The denticles on the inner lateral platform tend to be developed in a semi-transverse form, their outer edges being higher than their inner. They show semi-radiate development around the central point of the inner lateral platform, but this is not strongly marked in all individuals.

REMARKS. This subspecies was recognized as a distinct group by Meischner (1962) and Bouckaert & Higgins (1963).

Gnathodus girtyi soniae subsp. nov.

Plate 17, figs. 5a-8d

DERIVATION OF NAME. After Miss Sonia J. Kostromin.

DIAGNOSIS. Subspecies of *Gnathodus girtyi* resembling *G. girtyi girtyi* in having ornamentation developed continuously around posterior platform and encircling posterior termination of carina, but differing in development of 1 or 2 low rounded inconspicuous nodes on outer-anterior-lateral surface of platform.

MATERIAL. 18 specimens : Holotype X 113, Paratypes X 115, X 112, X 114 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample 3D 12.

RANGE. North Crop 3D 2-3D 14/15.

DESCRIPTION. A subspecies of *Gnathodus girtyi* with greatly expanded apron-like posterior platform, the sides sloping sharply down. The median carina is strongly developed and its posterior end is completely encircled by the lateral denticles of the platform. The inner-lateral parapet is the highest single feature of the platform ornament. It begins at a point anterior to the origin of the ornament, on the outer lateral side, and has 3 or 4 massive laterally elongate denticles, the highest of which tend to be those at the posterior end ; they are separated from the carina by a narrow sulcus, which opens anteriorly into a siphonodellid-like spout. The denticles decrease posteriorly in size, and are arranged as a linear series of low node-like forms.

On the outer-lateral margin of the platform one or two low rounded denticles are developed. These tend to be developed about midway along the length of the platform, and are visible but not conspicuous in lateral view.

The aboral cavity is large and flared, and the quadrangle outline of the outer lateral margin of some specimens is strongly reminiscent of *G. bilineatus*.

Gnathodus girtyi turritus Collinson & Druce

Plate 31, fig. 23

1957 *Gnathodus girtyi* Hass ; Bischoff : 24, 25, Pl. 4, figs. 18-20 (non figs. 16, 17, 22, 23 = *Gnathodus girtyi girtyi* Hass ; non pl. 4, fig. 21 = *G. girtyi simplex* Dunn).
Gnathodus girtyi turritus Collinson & Druce in press.

MATERIAL. 5 specimens : figured, X 116.

RANGE. North Crop 3D 19-3D 23.

DESCRIPTION. A subspecies of *G. girtyi* with a low posteriorly reduced carina. The lateral denticle ridges are generally continuous around the posterior edge of the platform. The sides of the posterior platform are nearly vertical.

REMARKS. The subspecies is extremely rare in our collections. Transitional specimens of *G. girtyi girtyi* are present in faunas from Yorkshire and the North Crop. It is difficult to refer these transitional specimens to one or other subspecies with any certainty.

Gnathodus girtyi subsp. nov. A

Plate 17, figs. 1a-3d

MATERIAL. 3 specimens : figured, X 117, X 118, X 119.

RANGE. North Crop CYD 7.

DESCRIPTION. A subspecies of *G. girtyi* characterized by the development of 1 or 2 vertical lateral pillars near the anterior inner end of the platform. The pillars extend from the oral surface almost to the aboral margin.

The three specimens upon which this new subspecies is based show the general features which are characteristic of *G. girtyi girtyi*. They differ from that subspecies, however, in being left forms in which the longer inner lateral denticulated margin of the platform is produced downwards by an unornamented, vertical column. In one specimen (Pl. 17, figs. 3a-d) this column reaches the aboral margin which is deflected by it. In this particular specimen the vertical pillar occurs about one quarter of the platform length behind the anterior end of the inner lateral denticle ridge. In the specimen illustrated in Pl. 17, fig. 1, the vertical pillar occupies the same relative position but is much less conspicuous, and the lateral margin only is conspicuously offset by it. In this specimen the oral margin of the denticulation is not disturbed in any way by a development of the lateral pillar. In the specimen shown in Pl. 17, fig. 2, two sharply angular vertical ridges are developed in the same relative position, but neither of these extends into the aboral margin ; between them there is a

regularly "U" shaped concave depression in the lateral face ; their upper terminations are bluntly pointed, and in this case they are joined to the main ridge of platform denticles by inconspicuous lateral ridges, although the denticle line is not broken by them. The ridge is not denticulated or ornamented in any obvious way in any of the three specimens.

REMARKS. It is possible that these three forms are pathological variants of *G. girtyi girtyi* but their restriction to a single sample and the fact that all three are left lateral forms makes this seem unlikely.

Gnathodus homopunctatus Ziegler

Plate 19, figs. 5a-8d

- 1957 *Gnathodus commutatus punctatus* Bischoff : 24, Pl. 4, figs. 7-11, 14.
 non 1957 *Gnathodus commutatus punctatus* Bischoff ; Ziegler in Flügel & Ziegler : 40 (Pl. 3, fig. 16 = juvenile of *Gnathodus bilineatus punctatus* (Cooper) 1939 ; Pl. 3, figs. 17, 24=*Gnathodus* sp.).
 1959 *Gnathodus commutatus homopunctatus* [Ziegler] Voges : 281.
 1960 *Gnathodus commutatus homopunctatus* Ziegler : 39, 5, Pl. 4, fig. 3 (*nom. nov.* for *Gnathodus commutatus punctatus* Bischoff 1957 non Cooper 1939).
 1961 *Gnathodus commutatus homopunctatus* Ziegler ; Higgins : Pl. 10, fig. 9, text-fig. 1c.
 1962 *Gnathodus commutatus homopunctatus* Ziegler ; Higgins : Pl. 2, fig. 21.
Gnathodus homopunctatus Ziegler ; Collinson & Druce in press.

MATERIAL. 146 specimens : figured, X 120-X 123.

RANGE. North Crop CYD 7-3D 14/15.

DESCRIPTION. There is some similarity and degree of transition between this species and *G. symmutatus*, but the present species differs in having a relatively shorter and more symmetrical posterior platform, with the development of more conspicuous denticulation. There is some variation in this denticulation ; in immature specimens (e.g. Pl. 19, fig. 5c) it is barely developed, and is present only as rather dark, slightly elevated lateral ridges. In other specimens it tends to be arranged at an acute angle to the anterior part of the blade, and consists only of short barb-like lines of denticles. In most specimens, however, it forms more or less symmetrical lines of low blunt denticles, developed parallel to the outer margin of the platform, about midway between its lateral margin and the position of the carina. In most individuals the development on the two sides of the carina is equal, but in others it is asymmetrical.

Gnathodus monodosus sp. nov.

Plate 19, figs. 13a-15d

- 1961 *Gnathodus commutatus* var. *nodosus* Bischoff ; Higgins : Pl. 10, fig. 7 only, text-fig. 1b.

DERIVATION OF NAME. From single node on the inner side of cup.

DIAGNOSIS. Straight to slightly curved blade with subcircular to sub-quadrangular cup, bearing strong, generally elongate node on inner side.

MATERIAL. 230 specimens : Holotype X 124, Paratypes X 125, X 126 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample 3D 14/15.

RANGE. North Crop CYD 7-3D 19.

DESCRIPTION. The blade is generally slightly curved. In lateral view both the oral and aboral outlines are nearly straight, although the anterior is slightly higher in some specimens. The denticles tend to be larger and more distinct at the anterior end and become increasingly small and fused toward the posterior. Most are fused to their tips. Both ends of the blade are nearly vertical in most specimens. The posterior end of the cup may project beyond the blade.

In oral view the cup is characteristically sub-quadrangular and slightly asymmetrical. The inner half bears a single node which is characteristically large and elongate but in some specimens round. The blade is typically more than twice the length of the cup.

REMARKS. This species is very close to *G. nodosus*. That it is not merely a random variant of *nodosus*, in which one or the other node is undeveloped, is shown by the fact that the single node occurs only on the inner side of the cup.

The present specimens tend to show all the main forms of variation exhibited in the platform by *G. commutatus*. They also show the rectangular profile of the blade of that species when seen in lateral view, and also the relative variation in the curvature and termination of the carina on the posterior end of the platform. In a very few specimens the outline of the platform is more reminiscent of *G. symmutatus*, but it differs from that species in having the square lateral profile of the blade, the oral surface being of more or less uniform height, and not showing the pronounced decrease in size of the posterior denticles over most of the length of the platform (see p. 108).

In a few specimens the inner platform is more elongate than in typical members of the species, the anterior margin being elongated at right angles to the line of the blade. These individuals are further distinguished by the presence of two denticles on the inner platform developed in a line lying at about 45° to the blade and pointing anteriorly, and both being rather laterally compressed and basally confluent but with more or less distinct apical tips. These specimens are so close in every other respect to those with a single denticle, that there seems no good reason for separating them.

In some specimens the denticle is not fully developed, but is represented by a slight swelling occupying the same relative positions on the inner lateral platform, and directed at about 45° to the anterior portion of the blade. There are transitions between this partial development of the denticle and full development of the denticle itself.

Gnathodus nodosus Bischoff

Plate 19, figs. 16a-20c

1957 *Gnathodus commutatus nodosus* Bischoff (*partim*) : 23-24, Pl. 4, figs. 12, 13.

1957 *Gnathodus commutatus nodosus* Bischoff ; Ziegler in Flügel & Ziegler : 40, Pl. III, fig. 4.

- 1958 *Gnathodus commutatus nodosus* Bischoff ; Lys & Serre : 891, Pl. 9, figs. 3a, b, 4a, b.
 1961 *Gnathodus commutatus* var. *nodosus* Bischoff ; Higgins (*partim*) : 213, Pl. 10, figs. 8
 (*non* fig. 7) ; text-fig. 1b (*non* figs. in lower left or in uppermost left).
 1962 *Gnathodus nodosus* Bischoff ; Higgins : Pl. 2, fig. 19.
 1962 *Gnathodus comm. nodosus* Bischoff ; Meischner : 31, text-fig. 10.
 1963 *Gnathodus commutatus nodosus* Bischoff ; Bouckaert & Higgins : 17, fig. 3.
Gnathodus nodosus Bischoff ; Collinson & Druce in press.

MATERIAL. 220 specimens : figured, X 509, X 510, X 127, X 128, X 129.

RANGE. North Crop 3D 10-3D 22.

DESCRIPTION. This species shows some characteristics with both *G. mononodosus* and *G. commutatus*. These include the posteriorly restricted laterally expanded sub-circular to asymmetrical platform, and the rectangular lateral profile of the uniform blade. The distinctive feature of the present species is the development of denticles on both sides of the posterior platform. These are generally unevenly developed, the one on the inner lateral side (represented by the concave lateral flexure of the blade) generally being the more strongly developed of the two. Where the denticles are more strongly developed, they tend to make angles of 45° with the anterior part of the blade and to be laterally elongate. In some specimens the outer lateral denticle is very feebly developed in comparison with the inner, but wherever there is a suggestion of such bilateral denticle development, specimens are included in the present species. Like the other species referred to above, this species shows considerable but continuous variation in the symmetry and degree of lateral expansion of the posterior platform, the form of the denticles, and the relationship of the posterior portion of the carina to the posterior end of the platform ; there is also variation in the degree of lateral deflection of the blade, and the outer lateral denticle may also be developed posterior to the position of the inner lateral denticle.

The blade is similar in general form to that of *G. commutatus* and *G. mononodosus*, having about 15 to 20 regular denticles, fused almost to their tips, and developing straight oral and aboral margins. There is a tendency in some specimens for the two anterior denticles to be relatively larger than the rest (e.g. Pl. 19, fig. 18a). The basal cavity is wide and flaring.

Gnathodus punctatus (Cooper)

Plate 18, figs. 1a-c, 10a-11d

- 1939 *Dryphenotus punctatus* Cooper : 386, Pl. 41, figs. 42, 43, Pl. 42, figs. 10, 11.
 1939 *Dryphenotus litus* Cooper : 386, Pl. 42, figs. 34, 35.
 1939 *Dryphenotus macrolobus* Cooper : 386, Pl. 41, figs. 48, 49 ; Pl. 42, figs. 45, 46.
 1939 *Dryphenotus oxys* Cooper : 386, Pl. 42, figs. 12, 13.
 1944 *Gnathodus (Dryphenotus) macrolobus* Cooper ; Branson & Mehl : 245, Pl. 94, fig. 69.
 1951 *Gnathodus punctatus* (Cooper) Hass : 2539, Pl. 1, fig. 2.
non 1957 *Gnathodus commutatus punctatus* Bischoff ; 24, Pl. 4, figs. 7-11, 14.
 1957 *Gnathodus bilineatus semiglaber* Ziegler in Flügel & Ziegler : Pl. 111, fig. 23 only.
non 1957 *Gnathodus commutatus punctatus* Bischoff ; Ziegler in Flügel & Ziegler : 40, Pl. 111, figs. 16, 17, 24.
 1959 *Gnathodus punctatus* (Cooper) Hass : 395, Pl. 47, figs. 11-18.

- 1959 *Gnathodus punctatus* (Cooper) Voges : 283-284, Pl. 33, figs. 34-37.
 1960 *Gnathodus punctatus* (Cooper) Kronberg, Pilger, Scherp & Ziegler : Pl. 4, figs. 15-18.
 1963 *Gnathodus punctatus* (Cooper) Ziegler : Pl. 2, fig. 4.

MATERIAL. 13 specimens : figured, X 131, X132, X 133.

RANGE. Avon Gorge Samples Z 33-38.

DESCRIPTION. This species is characterized by the adult specimens having the nodes of the inner and outer sides of the platform fused with those of the carina in the posterior two thirds of the platform. The pattern of nodes on the platform is also characteristic, there being four rows, radiating from the junction of the platform and blade. The platform is asymmetrical, being widest at the anterior end and pointed at the posterior ; the outer side is wider than the inner. In juvenile examples the carina is high, but in adult specimens the carina is fused with a row of nodes on the inner and outer sides of the platform. A double row of nodes is present on the outer side in fairly juvenile examples, but frequently there is only one row of nodes developed on the inner side in juveniles. The blade is slightly longer than the platform.

REMARKS. Hass (1959) has illustrated growth stages of this species. The specimens obtained in the present study most closely resemble those figured by Hass in Pl. 47, figs. 12, 13. Typically, the smaller inner side of the platform bears one node, whereas the wider outer side of the platform has a few scattered nodes. The outer side of the platform extends to the posterior tip of the unit. The inner side of the platform does not extend to the posterior tip of the unit, but extends further to the anterior than does the outer side of the platform.

In North America *Gnathodus punctatus* is abundant in the middle faunal zone of the Chappel Limestone, and also occurs in the *Siphonodella cooperi* and *Bactrognathus communis* zone. In the Avon Gorge it is characteristic of the Z₂ beds.

Gnathodus semiglaber Bischoff

Plate 30, fig. 1

- 1947 *Gnathodus perplexus* (Branson & Mehl) Mehl & Thomas : 10, Pl. 1, fig. 4.
 1957 *Gnathodus bilineatus semiglaber* Bischoff : 22, Pl. 3, figs. 1a, b, 2-10, 12-14.
 1957 *Gnathodus bilineatus semiglaber* Bischoff ; Ziegler in Flügel & Zeigler : p. 38, l. p111, figs. 5, 8, 14, 19 only (non pl. 111, fig. 23=*Gnathodus punctatus*, Pl. IV, fig. 11, non Pl. 3, fig. 22=*Gnathodus girtyi simplex* Dunn).
 1959 *Gnathodus semiglaber* Bischoff ; Voges : 285, Pl. 33, figs. 38, 39.
 1960 *Gnathodus semiglaber* (Bischoff) Ziegler in Kronberg, Pilger, Scherp & Ziegler : Pl. 4, figs. 3-6.
 1962 *Gnathodus semiglaber* (Bischoff) Collinson, Rexroad & Scott : 10, 22, Chart 3.
 1962 *Gnathodus semiglaber* (Bischoff) Higgins : 13, Pl. 3, fig. 26.
 1962 *Gnathodus semiglaber* (Bischoff) Müller : 1388, fig. 1.
 1962 *Gnathodus semiglaber* (Bischoff) Meischner : 31, text-fig. 10.
 1964 *Gnathodus semiglaber* (Bischoff) Rexroad & Scott : 30, Pl. 2, figs. 1, 2.

MATERIAL. 3 specimens : figured, X 421.

RANGE. Avon Gorge Z 28-Z 30.

DESCRIPTION. This species, which is well known and widely distributed in both Europe and North America, is characterized by a low, small parapet on the inner side of the platform, and a few scattered nodes developed on the middle part of the low outer side of the platform. The carina tends to be laterally expanded in the posterior part of the platform. Our specimens of this species agree closely with those described by other authors.

Gnathodus simplicatus sp. nov.

Plate 8, figs. 5a-c. Plate 18, figs. 2a-5b

1957 *Spathognathodus subrectus* Holmes ; Flügel & Ziegler : 53, Pl. 11, fig. 12.

1960 *Spathognathodus strigosus* Branson & Mehl ; Dvorak & Freyer : Pl. 1, fig. 17.

DERIVATION OF NAME. From the simple form.

DIAGNOSIS. A species showing *Spathognathodus*-*Gnathodus* transition, with characteristic anterior blade, its highest point being at or near the anterior end, and with oral surface sloping regularly towards the posterior end of unit. Platform very feebly developed.

MATERIAL. 105 specimens : Holotype X 89, Paratypes X 88, 90, 91, 415 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample ZLA 33.

RANGE. North Crop ZLA 15-ZLA 33, Avon Gorge Z 33-Z 38.

DESCRIPTION. The unit is slightly bowed and slightly arched, highest in the anterior quarter, and sloping posteriorly. The anteriormost one to three denticles may be slightly shorter than the penultimate denticles, but otherwise the oral outline is straight to slightly convex. The denticles, which number 13 to 15, are small and laterally compressed with free chevron tips. The basal cavity is situated in the posterior half and runs to the posterior termination ; the lips flare over the whole length and the cavity widens to the mid-point where it becomes constricted and then runs as a narrowing groove towards the anterior. The basal margin is lipped and slightly stepped in lateral view.

REMARKS. Middle and Upper Devonian forms similar to those described above have been named as *Spathognathodus bidentatus* by Bischoff and Ziegler (1957) and Freyer (1961). Bischoff and Ziegler's specimens have a greater number of denticles (about 17 total) than ours, and the cavity is different, not quite reaching the posterior end, and being greatly flared anteriorly. Freyer's specimens have only about 10 denticles and are much lower towards the posterior.

The present species is transitional between *Spathognathodus* and *Gnathodus*, but is included in *Gnathodus* because the basal cavity is developed posteriorly, is longitudinally extended, and the lips show a tendency to lateral flare.

There is some similarity between the forms described here and *S. cristulus*, which is considered by American workers to be the basic stock for all spathognathodid lineages. It is possible that the two species are the root stocks for successive gnathodid developments, the genus *Gnathodus* being polyphyletic.

In a few specimens the highest denticles are developed above the anterior end of the basal cavity (e.g. Pl. 18, fig. 2c ; X 89). In all other respects, however, these specimens resemble the holotype.

Gnathodus symmutatus sp. nov.

Plate 19, figs. 1a-4c

- ? 1941 *Spathognathodus commutatus* Branson & Mehl ; Ellison & Graves : Pl. 2, fig. 4 (non Pl. 2, fig. 6).
 ? 1956 *Spathognathodus* cf. *inornatus* Hass ; Elias : Pl. 3, figs. 62, 65 (non Pl. 3, figs. 41, 42).
 1958 *Gnathodus commutatus commutatus* Branson & Mehl ; Lys & Serre : 891, Pl. 9, figs. 2a, b.

MATERIAL. 42 specimens : Holotype X 134, Paratypes X 135-7.

TYPE LOCALITY AND HORIZON. North Crop Sample 3D 14/15.

RANGE. North Crop CYD 7-3D 22.

DIAGNOSIS. Small gnathodids with elongate blades, and relatively little expanded posterior platforms, convex in outline, tapering at both ends, and unornamented.

DESCRIPTION. The blade is more or less regular in height or has a gently convex oral profile in the anterior portion, but for most of the length of the platform the denticle height decreases uniformly towards the posterior end of the unit. In mature specimens the anterior blade occupies about half of the total length of the unit ; it is often deepest at its posterior end, and the oral surface bears about 9 or 10 denticles anterior to its junction with the posterior platform. These denticles tend to be more or less erect, discrete from about their mid points upwards, and sharply pointed ; they are strongly laterally compressed and are of sub-equal size, the largest tending to occur in the posterior portion of the anterior blade. The lateral faces of the bar are gently convex and the anterior aboral margin is rounded to bluntly angular ; the anterior edge is straight, and the bar is straight or gently deflected in a horizontal plane. The blade is continued posteriorly as a central carina on the platform, the denticles being short, and partly fused ; the total number of denticles in the blade and the carina is about 22. The posterior platform occupies the posterior half to two-thirds of the unit ; it is relatively unexpanded laterally and tapers uniformly at its anterior and posterior ends. It tends to be steep sided, the lateral faces forming an acute angle below the carina ; one face is often more strongly laterally expanded than the other. The surface is smooth and no ornamentation is developed, although in some specimens there is a tendency for the appearance of incipient marginal denticulation, similar to that in *G. homopunctatus*.

The basal cavity is wide and flaring, and is continued anteriorly as a narrow groove on the base of the anterior blade. The growth of the posterior platform in mature specimens tends to reduce the angle which its lateral faces form at their junction. In most specimens its depth is about equal to the height of the carina on its surface.

Gnathodus ? sp. nov.

Plate 18, figs. 7a-c

MATERIAL. 1 specimen : figured, X 92.

LOCALITY AND HORIZON. North Crop. Sample ZL 8.

RANGE. North Crop ZL 8.

DESCRIPTION. A gnathodid ? with transversely ridged posterior half of platform ; anterior part of platform unornamented except for marginal nodes. Base deeply excavated. Anterior bar unknown.

The anterior blade is broken but the platform is preserved. The carina consists of a row of low nodes ; in the posterior half of the platform, a row of smaller nodes runs either side of the carina, with which they fuse to give a series of trinodate transverse ridges. The inner platform is expanded slightly more than the outer, and both are unornamented, except for a short marginal row of fused nodes occurring in the anterior half and diverging posteriorly.

In aboral view the cavity occupies the whole area of the platform and is grooved along its mid-length.

REMARKS. This species is unlike any described gnathodid and does not bear any obvious phylogenetic relationship to other species.

Gnathodus sp.

Plate 17, figs. 4a-d

MATERIAL. 1 specimen : figured, X 138.

RANGE. Scotland HOSIE 2A.

DESCRIPTION. A single specimen of *Gnathodus* appears to be close to *G. girtyi*, but differs from it in the character of the lateral denticles of the posterior platform. In the present specimen the development on the two lateral areas of the platform is highly asymmetrical, and the platform of the inner-lateral margin, which begins anterior to the point of origin of that on the outer-lateral margin, is short, and consists of only three or four fused blunted denticles. Just anterior to its fusion with the carina, a less conspicuous fused, inner series of lateral denticles is developed on the outer-lateral platform. These become confluent with the carina just in front of its posterior termination, but do not reach the posterior end of the carina. The apron is wide and flaring, and is asymmetrical in both oral and aboral views. In lateral view the denticles of the anterior blade are sharp and erect, and those of the carina are also sharply tipped and distinct, standing higher than the lateral denticles on either side of the platform. The denticles of the inner lateral process form blunted parapet-like nodes in lateral view. The denticles of the carina decrease rapidly in size towards the posterior in the posterior half of the platform.

Genus *HIBBARDELLA* Ulrich & Bassler 1926

1925 *Hibbardella* Bassler ; 219 (*nom. nud.*).

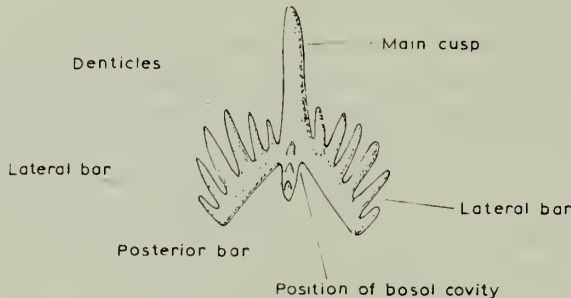
1926 *Hibbardella* Ulrich & Bassler : 37.

TYPE SPECIES. *Prioniodus angulatus* Hinde 1879.

DESCRIPTION. Ulrich & Bassler established the genus *Hibbardella* with the type species *Hibbardella (Prioniodus) angulata* Hinde for a group of arched blade-like conodonts in which a striking apical denticle was developed. The whole structure was bilaterally symmetrical and the apical denticle sharp-edged, erect and greatly elongated. The denticles of the anterior bar were relatively few in number, widely spaced and turned slightly inward. Ulrich & Bassler did not mention the character of the basal cavity, nor the possibility of the development of a denticulated posterior bar. Topotype material studied by Dr. J. W. Huddle, of which he has kindly provided us with photographs, shows that both these features are well preserved. A more or less short stout denticulated posterior bar is developed, and there is a thin groove-like basal cavity which extends along both the anterior bars and the posterior bar.

Subsequent authors have erected several genera of essentially similar general form which have been distinguished on minor morphological differences. These include *Roundya* Hass (1953) *Ellisonia* Müller (1956) and possibly also *Diplododella* Bassler (1925). There has been some discussion as to the validity of these and other genera, especially the genus *Trichonodella*. The most satisfactory solution to the present situation seems to be to subdivide the genus *Hibbardella* into three subgenera, based on the following characteristics :

1. *HIBBARDELLA* s.s. arched denticulated conodonts, with a bilaterally symmetrical anterior bar and a strongly developed apical denticle. The apical denticle is strongly compressed antero-posteriorly and has sharp



Anterior view

FIG. 23. *Hibbardella* sp. showing morphological terms used in the text.

lateral edges. The basal cavity is small and restricted to the aboral surface of the apical denticle, but aboral grooves are developed on both the anterior and the posterior bars. There is a short stout denticulated posterior bar, which bears a series of discrete denticles.

TYPE SPECIES. *Prioniodus angulatus* Hinde 1879.

2. **ROUNDYA** conodonts of similar overall form to *Hibbardella* s.s. but characterized by distinctive basal cavities and by the form of the apical denticle. The basal cavity is relatively much larger than that of *Hibbardella*, although it is still confined to the lower surface of the apical denticle. The whole aboral surface of that denticle is hollowed out, but the cavity does not flare beyond its basal area. The denticle itself is characterized by its distinctive cross-section. In its lower half it is broadly sub-circular and robust in form, the posterior surface having a longitudinal broad concave cavity which is deepest at the proximal end, and decreases in depth towards the mid-length of the denticle. The lateral faces of the apical denticle are smooth and strongly convex, but in their medial areas a conspicuous groove is developed longitudinally in the lower part. From this a strong lateral costa develops on each lateral face. In the distal half of the apical denticle it becomes strongly antero-posteriorly compressed, but the lateral edges remain sharp, and the anterior and posterior faces broadly convex.

TYPE SPECIES. *Roundya barnettana* Hass 1953.

3. **HASSOGNATHUS** subgen. nov. conodonts whose general form is similar to *Hibbardella*, but which are characterized by the fact that the anterior bars are essentially unexcavated, their aboral surfaces being shallow, concave, depressions. The basal cavity is conspicuous, but is largely developed below the posterior bar, although it extends and is continuous with one below the apical denticle. The apical denticle is usually sub-circular in cross-section and unornamented. The whole appearance of members of this subgenus is of a *Ligonodina* which has developed an additional lateral bar.

TYPE SPECIES. *Trichognathus separata* Branson & Mehl 1934.

Subgenus **HIBBARDELLA (HIBBARDELLA)** Ulrich & Bassler 1926

Hibbardella (Hibbardella) abnormis Branson & Mehl

Plate 31, fig. 6

1940 *Hibbardella abnormis* Branson & Mehl : 184, Pl. 6, fig. 14.

1963 *Hibbardella abnormis* Branson & Mehl ; Rexroad & Collinson 10, Pl. 2, figs. 15, 18, 20, 21.

1965 *Hibbardella abnormis* Branson & Mehl ; Rexroad & Collinson : 9, Pl. 1, figs. 8, 9.

MATERIAL. 3 specimens : figured, X 508.

RANGE. North Crop CYD 7-3D 8.

DESCRIPTION. Rexroad & Collinson (1963) have shown that the holotype of this species is broken and that the limbs are longer than the original description suggests.

The present specimens are fragmentary, but they show the specific characteristics. The posterior bar tends to be rather strongly developed, and the lateral bars are sharply flexed posteriorly.

Hibbardella (Hibbardella) acuta Murray & Chronic

Plate 25, figs. 19a-20

1961 *Hibbardella fragilis* Higgins : 213, Pl. 12, fig. 4, text-fig. 2.

1963 *Hibbardella fragilis* Higgins ; Bouckaert & Higgins : 17, fig. 3.

1965 *Hibbardella acuta* Murray & Chronic : 598, Pl. 73, figs. 3-5.

Hibbardella higginsii Collinson & Druce in press.

MATERIAL. 19 specimens : figured, X 139, X 422.

RANGE. North Crop 3D 4-3D 17.

DESCRIPTION. The most distinctive features of this species are the greatly elongated anterior and posterior bars, the relatively slender denticulation and the lateral twisting of the anterior bars. The apical denticle, although relatively long, is only about half the length of the anterior bars ; it is slender, with a feebly convex to flat anterior face and sharp lateral edges ; the posterior part of the face of the apical denticle is developed into a posterior knife edge, the posterior lateral faces tending to be rather flat. The anterior bars are long and are longitudinally twisted so that the denticles tend to originate from the anterior surface. The bars bear up to 10 lateral denticles which are basally confluent but apically distinct and are more or less compressed anterior-posteriorly. In addition to their longitudinal flexure, the bars are recurved posteriorly, so that their anterior faces are gently convex. They diverge from each other at an angle of about 30°.

The posterior bar is elongated and decreases in depth posteriorly. Its aboral margin is gently concave, most of the curvature being concentrated near the mid-point of the unit. Its oral surface bears a series of confluent, but apically distinct, hindeodellid-type denticles. The larger members of the series tend to increase in size toward the mid-point of the bar, and then to decrease toward the posterior end. There are about 8 or 9 main denticles, each separated by two or three smaller denticles. The denticles are more or less laterally compressed, but tend to have rather strong convex lateral faces. The lateral faces of the posterior bar are gently convex. The whole appearance of the posterior bar is strikingly deep and elongated.

Shallow longitudinal slit-like grooves extend along the anterior and posterior bars, and there is a very small pit below the apical denticle.

Hibbardella (Hibbardella) milleri Rexroad

Plate 25, figs. 23a-25b

- 1957 *Hibbardella* n. sp. ? Rexroad : 31, Pl. 1, fig. 19.
 1958 *Hibbardella milleri* Rexroad : 18, Pl. 2, figs. 13-16.
 1960 *Hibbardella milleri* Rexroad ; Clarke : 6, Pl. 1, fig. 6.
 1961 *Hibbardella milleri* Rexroad ; Higgins : Pl. 12, fig. 7.
 1961 *Hibbardella milleri* Rexroad ; Rexroad & Burton : 1153, Pl. 140, figs. 3, 4.
 1964 *Hibbardella milleri* Rexroad ; Rexroad & Furnish : 671, Pl. 111, fig. 17.
 1965 *Hibbardella milleri* Rexroad ; Rexroad & Nicoll : 19, Pl. 1, fig. 13.

MATERIAL. 3 specimens : figured, X 140, X 141, X 142.

RANGE. North Crop 3D 14/15.

DESCRIPTION. Individual specimens of this species bear a strong resemblance to those described by Rexroad, but differ from his description in having no denticle developed anterior to the apical denticle. The most characteristic features of individuals are the short, deep and obtusely divergent anterior bars, the distal ends of which are spatulate to sharply pointed. The denticles of the anterior bars are massive, increasing in size distally and numbering 3 or 4. They are more or less anteriorly compressed and sharp edged. The apical denticle is massive, elongate, sub-circular to oval in cross-section ; in some specimens it is very elongate (e.g. Pl. 25, fig. 24). In well preserved specimens the apical denticle is sharply pointed at its distal end, and is sub-circular in cross-section. In the proximal third its posterior surface is marked by either a very faint groove or a very faint depression. The posterior bar is short, narrow and deep, with two or three small, isolated denticles on its oral surface.

The basal cavity is developed as shallow grooves which run along the posterior and the anterior bars, and the base of the apical denticle is slightly excavated. The aboral groove does not extend the whole length of the anterior bars, and the posterior groove decreases in width and depth posteriorly.

Hibbardella (Hibbardella) ortha Rexroad

Plate 25, figs. 22a, b

- 1900 *Prioniodus angulatus* Hinde (*partim*) : 343, Pl. 10, fig. 18 (*non* fig. 19).
non 1926 *Hibbardella angulata* (Hinde) Ulrich & Bassler : 37, Pl. 3, figs. 1-4.
 1928 *Hibbardella angulata* (Hinde) ; Holmes : 11, Pl. 4, fig. 32.
 1958 *Hibbardella ortha* Rexroad : 18, Pl. 2, figs. 9-12.
 1960 *Hibbardella ortha* Rexroad ; Clarke : 6, Pl. 1, fig. 7.
 1961 *Hibbardella ortha* Rexroad ; Rexroad & Burton : 1153, Pl. 140, figs. 5, 6.
 1964 *Hibbardella ortha* Rexroad ; Rexroad & Furnish : 671, Pl. 111, fig. 16.
 1965 *Hibbardella ortha* Rexroad ; Rexroad & Nicoll : 19, Pl. 1, fig. 12.
Hibbardella ortha Rexroad ; Collinson & Druce in press.

MATERIAL. 780 specimens : figured, X 143.

RANGE. North Crop 3D 10-3D 22.

DESCRIPTION. The present specimens are more complete than those described by

Rexroad, but they agree in all the essential details with his description. Their most striking features are the deep and strongly antero-posteriorly compressed anterior bars, which diverge from each other at an angle of about 130° . They are relatively short, and bear on their oral surfaces up to 6 discrete and sharply pointed denticles. The two nearest the apical denticle and the distal denticle on each bar are small, but the three intervening denticles are larger and tend to increase in size distally. The ends of the anterior bar are bluntly spatulate, and the aboral margin is straight to feebly convex. The anterior face of the apical denticle is convex, the apical denticle itself being about twice the length of the largest denticle of the anterior bar, slender and pointed; it tends to have rather feeble anterior lateral edges in its lower portion, but becomes sub-oval in cross-section towards its distal end. Both it and the denticles of the anterior bar tend to stand rather erect to the bar itself and are not obviously posteriorly recurved, although the denticles of the lateral bar tend to be inwardly curved towards the apical denticle.

The posterior bar is long, slender, strongly laterally compressed and relatively deep. It has feebly convex lateral faces, and bears a series of up to 6 crowded, but apically discrete, laterally compressed, short denticles on its oral surface. A small pit below the apical denticle extends posteriorly as a faint groove along the posterior bar, and also along the proximal portions of the anterior bars. The posterior margin of the apical denticle is sharp-edged. Beneath the apical denticle the posterior-aboral margin of the anterior bar is excavated by an indented depression to join the basal margin of the posterior bar.

***Hibbardella (Hibbardella) parva* sp. nov.**

Plate 25, figs. 21a, b

DIAGNOSIS. Hibbardellid with very small, delicate structure; anterior bars flexed forwards diverging in vertical plane at a very obtuse angle. At their junction deeply indented aborally on anterior margin. Posterior bar strong; apical denticle elongate, strongly laterally compressed. Basal cavity minute or non-existent.

MATERIAL. 5 specimens: Holotype X 144 (figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample 3D 14/15.

RANGE. North Crop 3D 14/15.

DESCRIPTION. The anterior bars are relatively deep, short and laterally compressed, and each bears about 5 oral denticles. They diverge anteriorly in a horizontal plane, so that the angle between them in a horizontal plane is about 90° . They are little flexed in a vertical plane, and the angle between them is very obtuse. The aboral surface has a concave general appearance. This anterior curvature is most obvious in aboral view. It is relatively inconspicuous in oral view, where it is obscured by the development of the apical denticle, nor is it continued along the medial and distal parts of the bars which tend to straighten out and lie in a single plane relative to one another.

REMARKS. This species is closest to *H. (H.) ortha* Rexroad 1958, but it differs in

the distinctive form of the apical denticle, and in the characteristic angle of the anterior bars as seen in the vertical plane. In *H. (H.) ortha* this angle approaches 90° but it is nearer 180° in *H. (H.) parva*. *H. (H.) ortha* also lacks the strong posterior recurvature of the apical denticle and the denticles of the anterior bar.

***Hibbardella (Hibbardella) cf. macrodentata* Thomas**

Plate 25, figs. 16a-18c

1949 *Hibbardella macrodentata* Thomas : 422, Pl. 4, fig. 25.

MATERIAL. 75 specimens : figured, X 147, X 148, X 146.

RANGE. North Crop KL 2-ZLA 33, Avon Gorge K3-Z 38.

DESCRIPTION. The apical denticle is tall, laterally compressed and inclined posteriorly. The anterior arch is deep with each limb curved posteriorly. The anterior bars diverge at an angle of approximately 90°, and the aboral edge of the anterior bars is lower than that of the posterior bar. The denticles of the arch are isolated, sub-circular and of unequal height. The posterior bar is narrow, long (though broken in the majority of our specimens) and finely denticulate. All the denticles are sub-circular and posteriorly inclined. The cavity is minute and situated beneath the apical denticle.

REMARKS. The holotype is broken, but, from Thomas's illustration and description it would appear that our specimens are very close to *H. macrodentata*. Although Thomas describes the posterior bar as blunt and non denticulate, the holotype (shown in Pl. 4, fig. 25) is clearly broken.

Hibbardella (Hibbardella) sp.

Plate 25, figs. 15a, b

MATERIAL. 1 specimen : figured, X 441.

RANGE. North Crop KL 16.

DESCRIPTION. This specimen is characterized by the massive form of its anterior bars. The anterior bars are short, deep and strongly downcurved, their oral and aboral margins being strongly convex in anterior view, although there is a conspicuous indentation in the aboral profile below the apical denticle. The strongest downflexing is in the distal thirds of the bars. The lateral faces of the anterior bars are convex, and both are characterized by prominent longitudinal ridges developed just below mid-height, and extending along the length of the bars. The oral surfaces of the anterior bars bear up to six discrete and rather stout denticles, the largest being in the medial portions of the bars. They are discrete, more or less rounded in cross-section, and the larger ones are slightly inflexed towards the apical denticle. Their length is unknown, but the largest is longer than the depth of the basal bars. The ends of the bar are spatulate.

The apical denticle is relatively slender, being only slightly greater in width than the largest of the denticles of the anterior bars. The anterior face is rounded, but

the posterior face is blunt and has a median groove. The apical denticle in posterior view is widest at the oral edge of the bar and tapers uniformly to the tip.

The aboral surface is sharp, being broken only by a small triangular shaped pit directly beneath the apical denticle.

Subgenus *HIBBARDELLA (ROUNDYA)* Hass 1953

TYPE SPECIES. *Roundya barnettana* Hass 1953.

Hibbardella (Roundya) barnettana Hass

Plate 25, figs. 2a-5b

- 1953 *Roundya barnettana* Hass : 89, Pl. 16, figs. 8, 9.
 1957 *Roundya barnettana* Hass ; Bischoff : 52, Pl. 5, figs. 19, 20.
 1958 *Roundya costata* Rexroad : 26, Pl. 2, figs. 5-8.
 1961 *Roundya subacoda* (Gunnell) Higgins : 220, Pl. 11, fig. 13.
 1961 *Roundya costata* Rexroad ; Rexroad & Collinson, Pl. 1.
 1962 *Roundya subacoda* (Gunnell) Higgins : 11, Pl. 1, fig. 1.
 1962 *Roundya barnettana* Hass ; Collinson, Scott & Rexroad : 12.

MATERIAL. 14 specimens : figured, X 151, X 152, X 153, X 154.

RANGE. North Crop 3D 14/15, Avon Gorge Z 38-C 15.

DESCRIPTION. Individuals of the present species agree closely with the very detailed description given by Hass (1953 : 89). They are characterized particularly by the massive apical denticle, with longitudinal grooves and lateral keels which are very prominent in the proximal portion, and sharp lateral edges which are prominent in the distal half. There is a conspicuous posterior concave longitudinal depression in the proximal quarter of the apical denticle, which becomes obsolescent towards the mid-point. The denticle is strongly recurved in its lower portion, but its distal portion is straight. The anterior bars are broken in the present specimens, but appear massive and bear more than two isolated denticles, which are sub-circular in cross-section, and curve upwards to parallel the apical denticle. The anterior bars diverge at an angle of about 70°-80° in the vertical plane, and the junction between them is rounded in anterior view. They shallow distally. The posterior bar is broken in the present specimens, but is clearly massive with flat to gently convex lateral faces, and has a convex upper surface which bears more than one erect, massive, sub-circular denticle.

The aboral surface of the apical denticle is deeply excavated and the excavation continues along the anterior end of the posterior bars.

Hibbardella (Roundya) sp.

Plate 25, fig. 1

MATERIAL. 2 specimens : figured, X 423.

RANGE. North Crop ZLA 32.

DESCRIPTION. The anterior arch is broken but appears to be formed by aboro-lateral extensions of the basal cavity. The apical denticle is recurved posteriorly ; it has a convex anterior margin, lateral keels, and a concave posterior depression, becoming obsolescent toward the anterior arch. The posterior bar is formed by an extension of the posterior lip of the basal cavity and bears at least one inclined denticle.

The basal cavity is large, the aboral region of the apical denticle being completely excavated.

Subgenus *HIBBARDELLA* (*HASSOGNATHUS*) nov.

TYPE SPECIES. *Trichognathus separata* Branson & Mehl 1934.

Hibbardella (*Hassognathus*) *separata* (Branson & Mehl)

Plate 25, figs. 13a-14

- 1934 *Trichognathus separata* Branson & Mehl : 290, Pl. 23, fig. 30.
 1934 *Trichognathus breviolata* ? Branson & Mehl : 291, Pl. 23, fig. 29.
 1938 *Trichognathus separata* Branson & Mehl ; Branson & Mehl : Pl. 33, fig. 42.
 1939 *Trichognathus separata* ? Branson & Mehl ; Cooper : 421, Pl. 46, figs. 45, 49.
 1944 *Trichognathus separata* Branson & Mehl ; Branson & Mehl, in Shimer & Shrock : 243, Pl. 93, fig. 72.
 1944 *Trichognathus separata* Branson & Mehl ; E. B. Branson : Pl. 32, fig. 42.
 1959 *Roundya* sp. B Hass : 385, Pl. 46, fig. 11.

MATERIAL. 58 specimens : figured, X 150, X 149.

RANGE. North Crop KL 19-ZLA 27, Avon Gorge K 21-C 17.

DESCRIPTION. The posteriorly recurved apical denticle is tall and ovate in cross-section, being thickest at the anterior. The anterior arch is short with the anterior bars diverging at about 120°. The bars are narrow, each bearing 3 to 4 short, sub-circular posteriorly inclined denticles. The posterior bar is relatively long, being thick at the anterior end, and becoming much thinner over the posterior half, where it bears a few fine posteriorly inclined denticles.

In aboral view the unit is excavated, with a large cavity occurring beneath the apical denticle and extending along the posterior bar, but becoming gradually narrower and ending abruptly. A faint groove runs for a short distance from the cavity along either limb of the anterior arch.

REMARKS. The large basal cavity distinguishes this species from *H. macrodentata*.

Hibbardella (*Hassognathus*) ? sp.

Plate 31, fig. 3

MATERIAL. 1 specimen : figured, X 319.

RANGE. Scotland DUN 77.

DESCRIPTION. The present specimen is fragmentary but has a very distinctive appearance. The posterior bar is elongated and tapers towards the posterior end. The main cusp is strongly recurved and strongly laterally compressed in its distal half, the proximal half tending to be more rounded. Posterior to it there is a denticle adding about a third of the total length of the main cusp, and the denticles posterior to this decrease in size posteriorly. They are short, bluntly pointed and discrete. The aboral surface of the posterior bar is straight, and the oral surface curves down to meet it. The two lateral bars are developed well in front to the line of the main cusp, so that the general appearance of the unit in lateral view resembles that of a *Ligonodina*. They are not down-flexed and their aboral margin is in line with that of the posterior bar. They make an angle of about 90° with the posterior bar in a horizontal plane. They share a single short, but stout, recurved denticle, which lies directly anteriorly to the main cusp.

The aboral surface of the posterior bar is excavated by a wide elongate depression. The whole margin tapers towards the posterior end. There is no conspicuous cavity below the main cusp.

REMARKS. One distinctive feature of this specimen is the presence of the denticle anterior to the main cusp. This might ultimately justify the recognition of specimens of this kind as a new genus, but our present material is inadequate to provide a full description. Other fragmentary, but different, hassognathids have a much greater stratigraphic range.

Genus *HINDEODELLA* Ulrich & Bassler 1926

1925 *Hindeodella* Bassler : 219 (*nom. nud.*).

1926 *Hindeodella* Ulrich & Bassler : 38-41.

TYPE SPECIES. *Hindeodella subtilis* Ulrich & Bassler 1926.

Hindeodella antecomplex Collinson & Druce

Plate 28, figs. 25, 28

Hindeodella antecomplex Collinson & Druce in press.

MATERIAL. 7 specimens : figured, X 157, X 156.

RANGE. North Crop 3D 4-3D 17.

DESCRIPTION. The present specimens agree closely with the description given by Collinson & Druce. The most striking features of the specimens are their small size, the general form of the main denticle, which is relatively massive in relation to the general size of the unit, being curved posteriorly and inwardly with a very convex interior antero-lateral face. The denticles of the posterior bar range up to about 10 in number, and the two massive posterior denticles are very prominent in lateral view. The denticles show a general increase in size posteriorly, as does the depth of the posterior bar. The aboral margin of the posterior bar is straight, and each of its aboral lateral surfaces is marked by a flange-like structure. The anterior lateral

process is short, and bears two oral denticles. It is strongly depressed vertically and strongly inflexed, forming a right angle in its lateral curvature with the posterior bar when viewed from above. The aboral surface of the unit is excavated by a narrow, shallow, groove.

Hindeodella brevis Branson & Mehl

Plate 31, fig. 17

1934 *Hindeodella brevis* Branson & Mehl : 195, Pl. 14, figs. 6, 7.

1934 *Hindeodella* cf. *brevis* Branson & Mehl : Pl. 14, fig. 12.

1956 *Hindeodella brevis* Branson & Mehl ; Bischoff & Ziegler : 147, Pl. 14, figs. 10, 11.

1957 *Hindeodella brevis* Branson & Mehl ; Bischoff : 26, 27, Pl. 6, fig. 24.

MATERIAL. 17 specimens : figured, X 514.

RANGE. Avon Gorge K 2-Z 38, North Crop 3D 14/15-3D 22.

DESCRIPTION. The posterior bar is short, deep, straight and relatively thick at its oral edge. It bears on its oral surface four or five major denticles, which increase in size posteriorly. They tend to be straight, strongly biconvex in cross-section, and only slightly inclined posteriorly. Each is separated by up to 3 smaller denticles, which are crowded but discrete. The anterior bar is relatively long, and is bent almost at right angles to the posterior bar. Its oral surface bears up to 7 short denticles, which decrease in size posteriorly. Each of these major denticles of the anterior process tends to be separated by a single smaller denticle. The posterior bar is excavated by a shallow groove in its anterior portion, and this flares somewhat below the main denticle.

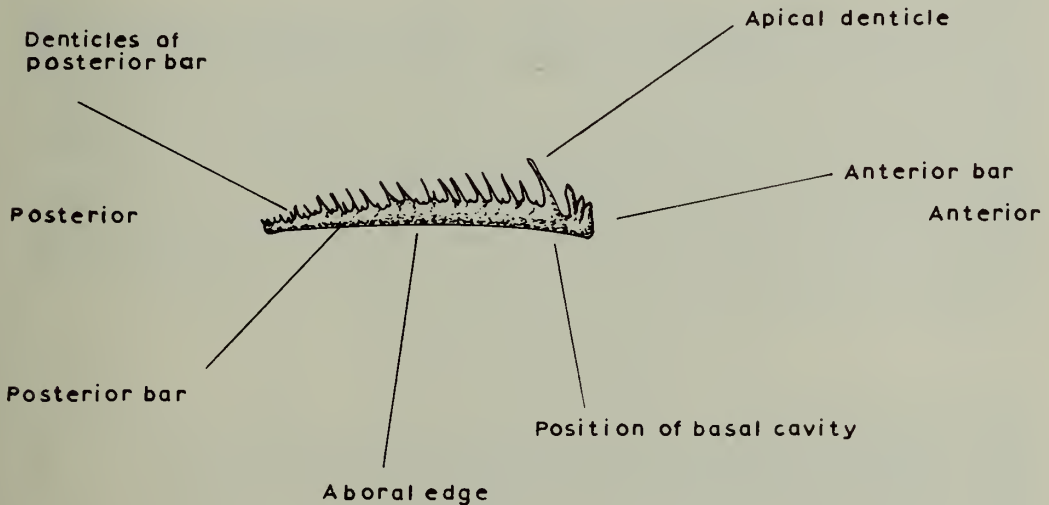


FIG. 24. *Hindeodella* sp. showing morphological terms used in the text.

Hindeodella cooperi (Elias)

Plate 31, figs. 18, 19

1956 *Hamulosodina cooperi* Elias : 109, Pl. 1, figs. 28, 29.
Hindeodella cooperi (Elias) ; Collinson & Druce in press.

MATERIAL. 2 specimens : figured, X 159, X 158.

RANGE. North Crop 3D 14/15.

DESCRIPTION. The original description of this species is scarcely adequate to differentiate it from several others of the genus *Hindeodella*. The most distinctive features of the present specimens, and also of the specimens shown in Elias' illustrations, are the greatly elongated posterior bar, the more or less subequal character of the denticulation, and the character of the antero-lateral process. The height of the denticle is consistent although major denticles can be identified in some parts of the bar. The anterior-lateral process is short, vertically depressed, slightly laterally deflected, and bears 1 to 4 denticles anterior to the main denticle, with the whole of the antero-lateral face undenticulated, and a more or less sharp convex edge.

In lateral view the aboral surface of the unit is straight to gently concave. Its outer face is flat to steeply convex in the anterior part, but becomes more strongly convex in the medial and posterior part. The main denticle is not conspicuously larger than those which lie behind it. The denticles of the main part of the posterior bar are crowded and fused for most of their length, being slightly inclined posteriorly and tending to increase slightly in size towards the mid-point of the unit in some specimens. In other specimens the main denticle is up to twice as large as the main denticles of the posterior series, and in the latter, the hindeodellid character is more or less conspicuously developed. The inner lateral face of the unit is flat to gently convex.

The antero-lateral process makes an angle of about 90° with the posterior bar. Its postero-aboral edge is straight and points vertically, and makes an antero-aboral angle at the anterior edge of about 45°. The denticles anterior to the main denticle tend to be about equal in height to those of the major denticles of the posterior bar, and curve upwards to lie more or less parallel to the main denticle. The lowermost anterior edge of the antero-lateral process is undenticulate.

The posterior bar is strongly laterally compressed. Beneath the main denticle there is a cavity which flares slightly at the edges, and this is extended posteriorly, and to a less extent, anteriorly as a narrowing groove.

Hindeodella corpulenta Branson & Mehl

Plate 29, figs. 16a-17c

- 1934 *Hindeodella* sp. Branson & Mehl : Pl. 14, fig. 15.
 1934 *Hindeodella corpulenta* Branson & Mehl : 281, Pl. 22, figs. 32, 33.
 1934 *Metaproniodus fractus* Huddle : 58, Pl. 11, figs. 14, 15.
 1934 *Ligonodina conidens* Huddle : 63, Pl. 12, figs. 18, 19.
 1938 *Ligonodina angulata* Branson & Mehl : 142, Pl. 34, fig. 43.
 1939 *Ligonodina conidens* Huddle ; Cooper : 390, Pl. 45, fig. 45.

- 1944 *Ligonodina angulata* Branson & Mehl ; E. B. Branson : Pl. 39, fig. 43.
 1947 *Hindeodella millerella* ? Youngquist & Peterson : 245, Pl. 38, figs. 1-5.
 1949 *Hindeodella* cf. *Hindeodella corpulenta* Branson & Mehl ; Thomas : 408, Pl. 1, fig. 4.
 1957 *Hindeodella* ? sp. Lys, Serre & Deroo : 800, Pl. 9, fig. 1.

MATERIAL. 168 specimens : figured, X 160, X 161.

RANGE. North Crop KL 1-ZLA 33, Avon Gorge K 2-Z 37.

DESCRIPTION. The main denticle is massive with a sub-circular cross-section at the oral extremity. It is ovate at its base, feebly recurved and posteriorly inclined. It is about one and a half times as wide as the next largest denticle. The anterior lateral process is deflected laterally through 90°, and depressed downward through 90°. It commonly bears 6 isolated, sub-circular denticles, which increase in size in the mid part. The posterior bar is massive, laterally compressed and bears about 5 massive, discrete, feebly laterally compressed, posteriorly inclined denticles, the largest being in the posterior third. No smaller "hindeodellid" denticles are present. The posterior bar is deflected downward slightly towards the posterior end.

In aboral view the large cavity is situated just anterior to the main denticle, and extends beneath the anterior lateral process. It is grooved along its mid-length. The inner lateral face may bear a feeble longitudinal ridge.

REMARKS. Most specimens of this species have the posterior bar broken, but the distinctive anterior lateral process and the basal cavity serve to identify it.

Hindeodella croka Collinson & Druce

Plate 28, figs. 15-17

- 1957 *Hindeodella brevis* Branson & Mehl ; Bischoff : 26, Pl. 6, fig. 24.
 1961 *Hindeodella brevis* Branson & Mehl ; Higgins : Pl. 10, fig. 14.
Hindeodella croka Collinson & Druce in press.

MATERIAL. 7 specimens : figured, X 164, X 162, X 163.

RANGE. North Crop 3D 9-3D 14/15.

DESCRIPTION. The distinctive elongate form and enormously flexed anterior lateral process of the species are very distinctive features, and agree in all respects with the description of Collinson & Druce. There is a tendency in some specimens for the posterior bar to develop broadly hindeodellid denticulation, but this is not very clearly defined. In some specimens the anterior lateral process bears up to 8 denticles.

REMARKS. A single specimen (Pl. 28, fig. 29) is compared with this species, differing from it in the very strong lateral extension of the inner lateral face of the unit. It is extended laterally along the whole length of the unit posterior to the origin of the anterior lateral process, forming a platform-type flange, with a rather flat, oral surface and a convex to vertical outer lateral face. The relatively inconspicuous main denticle is strongly inflexed, downflexed and less strongly recurved.

Hindeodella hibbardi Collinson & Druce

Plate 28, figs. 18-20

1957 *Angulodus walrathi* (Hibbard) Bischoff : 17, Pl. 5, figs. 44, 45.1961 *Angulodus walrathi* (Hibbard) Higgins Pl. 10, fig. 16.*Hindeodella hibbardi* Collinson & Druce in press.

MATERIAL. 22 specimens : figured, X 167, X 168, X 169.

RANGE. North Crop 3D 11-3D 14/15.

DESCRIPTION. This species of *Hindeodella* is characterized by a relatively long anterior lateral process, which is one third to one quarter the length of the posterior bar, and which is depressed and deflected at the bottom. Immediately anterior to the main denticle the anterior lateral process is depressed at an angle of about 110° to the posterior bar. Then, at a distance of about one quarter of its total length from the main denticle, it is inflexed by lateral twisting, so that the denticles anterior to this point of inflection point both inwards and also are curved upwards. At a further point about two-thirds of its length from the main denticle, it is again depressed in a vertical plane, and the remaining 3 distal denticles of the anterior lateral process are larger and more strongly recurved than those behind them. The oral surface of the anterior lateral process bears up to 10 stout denticles, more or less sub-circular in cross-section, discrete, tending to increase in size distally from the main denticle, although the most anterior is smaller than those immediately behind it. The process becomes thinner towards the anterior end, the antero-aboral extremity being bluntly rounded or plough-like in general form. The proximal end of the anterior lateral process and virtually the whole length of the posterior bar have conspicuously and strongly convex lateral faces. The denticles of the posterior bar are strongly developed, and curve inward, being inclined posteriorly at an angle of about 45° . The denticles of the main series are each separated by up to 4 smaller, fused, crowded denticles, which are less than half the length and diameter of those of the larger series. The posterior third of the unit is slightly depressed vertically and is deflected laterally.

A very conspicuous aboral groove runs the whole length of the unit, being wide but rather shallow, and having conspicuous lateral lips. It is reduced in width towards the anterior and posterior end, and is widest below the main denticle where it is marked by a more or less conspicuous biconvex pit, both ends of which are relatively pinched in relation to the rest of the cavity. The outer lateral face is rather less convex than the inner.

The main denticle is relatively small and inconspicuous in comparison with other denticles of the series. The whole unit is elongate, but in some specimens the lateral faces tend to be less convex than others, giving the whole unit a more slender appearance. In complete specimens the aboral cavity is seen to extend only for about half the length of the posterior bar.

Hindeodella ibergensis Bischoff

Plate 28, figs. 22-24, 30, 31

- 1957 *Hindeodella ibergensis* Bischoff : 28, Pl. 8, figs. 33, 37, 39.
 1957 *Hindeodella ibergensis* Bischoff ; Ziegler in Flügel & Ziegler : 42, Pl. 5, figs. 14, 21.
 1957 *Hindeodella germana* Holmes ; Ziegler in Flügel & Ziegler : 41, Pl. 5, fig. 16.
 1958 *Hindeodella redunca* Stanley : 466, Pl. 63, figs. 1-4.
 1961 *Hindeodella ibergensis* Bischoff ; Higgins : Pl. 10, fig. 15.
 1962 *Hindeodella ibergensis* Bischoff ; Higgins : Pl. 1, fig. 11.
 1963 *Hindeodella ibergensis* Bischoff ; Bouckaert & Higgins : 17, fig. 3.
Hindeodella ibergensis Bischoff ; Collinson & Druce in press.

MATERIAL. 37 specimens : figured, X 170, X 171, X 172, X 173, X 174.

RANGE. North Crop 3D 10-3D 19.

DESCRIPTION. This species includes greatly elongate hindeodellids, with the oral edge crowded with a series of alternating denticles. The aboral edge is straight to sinuous. In complete specimens the posterior bar decreases in width progressively towards the more or less pointed posterior tip. The main denticle is distinct, incurved and posteriorly deflected through 45° , being about twice the diameter of the largest denticles of the main posterior series. The antero-lateral process is short, its total length being only about one eighth to one tenth that of the posterior bar. Its postero-aboral edge makes an angle of approximately 90° with that of the posterior bar immediately adjacent to it. Its anterior inner edge is flexed slightly inwards and there is a series of 3 or 4 recurved, inwardly inclined denticles, which are more or less discrete pointed, and decrease in size towards the distal end, which is sharply pointed. Both the degree of "hindeodellid" alternation of the denticles of the posterior bar and the posterior inclination of the denticles show considerable variation, as also does the degree of convexity of the lateral faces of the posterior bar, which tends to increase posteriorly. All denticles of the posterior bar are either very closely spaced or fused for most of their length, the 3 or 4 which form the posterior end lying almost horizontally.

REMARKS. The only substantial difference between this species and *H. cooperi* is the distinctive denticulation of the anterior lateral process, which in the present species extends as far as the aboral tip of the bar, in contrast to *H. cooperi* where it is restricted to the proximal part.

Hindeodella montanaensis (Scott)

Plate 28, figs. 21, 26

- 1942 *Lochreia montanaensis* Scott (*partim*) : Pl. 39, fig. 7, Pl. 40, fig. 18 (*non* pl. 39, figs. 1, 4, 9 ; Pl. 40, figs. 2, 9, 10, 12, 13, 15, 19).
 1956 *Hindeodella bigeniculata* Elias (*partim*) : 106, Pl. 1, figs. 20, 21 (*non* Pl. 1, fig. 16).
 1956 *Hindeodella mehli* Elias : 108, Pl. 1, figs. 22-24.
 1957 *Hindeodella germana* Holmes ; Bischoff (*partim*) : 27, Pl. 6, fig. 32, (*non* Pl. 6, fig. 34 = *H. secarata* Collinson & Druce).
 1958 *Hindeodella montanaensis* (Scott) Stanley (*partim*) : 465, Pl. 64, figs. 1-5.

- 1961 *Hindeodella germana* Holmes ; Higgins (*partim*) : Pl. 10, fig. 12, (*non* Pl. 10, fig. 13=*H. secarata* Collinson & Druce).
Hindeodella montanaensis (Scott) ; Collinson & Druce in press.

MATERIAL. 80 specimens : figured, X 175, X 176.

RANGE, North Crop 3D 10-3D 19.

DESCRIPTION. Members of this species are slightly constructed hindeodellids, having a massive main denticle with a very wide base, strongly convex lateral faces, and being inclined posteriorly at an angle of about 45°. The denticles on the posterior bar are minute in comparison with this denticle. They are crowded and laterally compressed, with sharp anterior and posterior edges, having a hindeodellid pattern with 2 or 3 smaller denticles between the larger ones. The lateral faces of the posterior bar are gently to strongly convex. The anterior lateral process is deep with three confluent denticles near its proximal end, but the distal end, which points strongly upward and inward, consists of a single fang-like denticle, about half the width of the main denticle. The basal anterior and posterior edges of the main denticle are also minutely denticulate. The outer lateral surface of the main denticle is flat. The aboral surface of the whole unit is excavated by a shallow groove which flares below the main denticle. The posterior bar is straight and about 5 to 6 times the length of the anterior bar in the present specimens, but these are broken. One specimen, which is also broken, shows a tendency for the denticles near the posterior end of the bar to be relatively larger, about twice as large as most of the denticles of the posterior bar, although the aboral cavity is little expanded below the main denticle.

Hindeodella secarata Collinson & Druce

Plate 29, figs. 11, 13-15

- 1957 *Hindeodella germana* Holmes ; Bischoff (*partim*) : 27, Pl. 6, fig. 34 (*non* Pl. 6, fig. 32=*H. montanaensis*).
 1961 *Hindeodella germana* Holmes ; Higgins (*partim*) : Pl. 10, fig. 13 (*non* Pl. 10, fig. 12=*H. montanaensis*).
 1963 *Hindeodella germana* Bischoff ; Bouckaert & Higgins ; 17, fig. 3.
Hindeodella secarata Collinson & Druce in press.

MATERIAL. 46 specimens : figured, X 184, X 181, X 182, X 183.

RANGE. North Crop 3D 8-3D 19.

DESCRIPTION. The present specimens agree closely with the description given by Collinson and Druce. The posterior bar is greatly elongated and tends to taper towards the posterior end. It is straight to arched, with fine acicular denticles, and it lacks a well-developed anterior fang. The anterior process is very small, and is relatively feebly inflexed. The basal groove is conspicuous, but there is no obvious basal cavity at the anterior end.

Hindeodella subtilis Ulrich & Bassler

Plate 29, figs. 6a-7b, 9-10b

- 1926 *Hindeodella subtilis* Ulrich & Bassler : 39, Pl. 8, figs. 17-19.
 1927 *Hindeodella deflecta* Hibbard : 207, fig. 40.
 ? 1928 *Hindeodella germana* Holmes : 25, Pl. 9, fig. 9.
 1928 *Hindeodella subtilis* Ulrich & Bassler ; Pl. 9, figs. 10, 11.
 1931 *Hindeodella subtilis* Ulrich & Bassler ; Cooper : 147, Pl. 20, fig. 9.
 ? 1931 *Hindeodella pumilla* Cooper : 236, Pl. 28, fig. 18.
 ? 1931 *Hindeodella subtilita* Cooper : 236, Pl. 28, fig. 17.
 1932 *Hindeodella subtilis* Ulrich & Bassler ; Bassler : Pl. 26, fig. 21.
 1934 *Hindeodella delicatula* Branson & Mehl : 280, Pl. 22, fig. 30.
 1934 *Hindeodella alternidens* Huddle : 44, Pl. 5, fig. 13 (*non* Pl. 5, fig. 12 = *Hindeodella* sp.).
 1934 *Hindeodella angulus* Huddle : 44, Pl. 5, fig. 15.
 1934 *Hindeodella aculeata* Huddle : 40, Pl. 4, fig. 19 (*non* Pl. 4, figs. 20, 21 = *Hindeodella* sp. cf. *H. similis* Ulrich & Bassler), Pl. 5, figs. 2, 3.
 1934 *Hindeodella grandis* Huddle : 41, Pl. 4, fig. 22.
 ? 1934 *Hindeodella laticlavis* Huddle : 43, Pl. 5, figs. 9, 10.
 1935 *Hindeodella subtilis* Ulrich & Bassler ; Cooper : 309, 310, Pl. 27, fig. 27.
 1935 *Hindeodella germana* Holmes ; Cooper : 310, Pl. 27, fig. 25.
 ? 1935 *Hindeodella pumilla* Cooper ; Cooper : 310, Pl. 27, fig. 26.
 ? 1935 *Hindeodella subtilita* Cooper ; Cooper : 310, Pl. 27, fig. 28.
 1938 *Hindeodella delicatula* Branson & Mehl ; Branson & Mehl, Pl. 33, fig. 34.
 ? 1939 *Hindeodella lineata* (Pander) Cooper : 389, Pl. 46, figs. 28, 31.
 1939 *Hindeodella delicatula* ? Branson & Mehl ; Cooper : 389, Pl. 46, fig. 33.
 1939 *Hindeodella acuta* Branson & Mehl ; Cooper : 389, Pl. 46, figs. 15, 23, 29.
 1940 *Hindeodella moweri* Stauffer : 424, Pl. 58, figs. 2, 10, 11.
 1943 *Hindeodella subtilis* Ulrich & Bassler ; Cooper & Sloss : 170, Pl. 28, figs. 22, 32, 33.
 1943 *Hindeodella atteridens* Huddle ; Cooper & Sloss : 170, Pl. 28, fig. 23.
 1943 *Hindeodella petila* Cooper ; Cooper & Sloss : 170, Pl. 28, figs. 26, 35.
 1943 *Hindeodella deflecta* Hibbard ; Cooper & Sloss : 170, Pl. 28, figs. 27, 34.
 1943 *Hindeodella germana* Holmes ; Cooper & Sloss : 170, Pl. 28, fig. 28.
 1943 *Hindeodella grandis* Huddle ; Cooper & Sloss : 170, Pl. 28, figs. 31, 37, 39.
 1943 *Hindeodella laticlavis* Huddle ; Cooper & Sloss : 170, Pl. 28, fig. 38.
 1945 *Hindeodella aculeata* Huddle ; Cooper : 613, Pl. 84, figs. 7, 9.
 1945 *Hindeodella rotunda* Hibbard ; Cooper : 614, Pl. 84, fig. 8.
 1945 *Hindeodella grandis* Huddle ; Cooper : 614, Pl. 84, fig. 10.
 1945 *Hindeodella gracilis* Huddle ; Cooper : 614, Pl. 84, fig. 11.
 1945 *Hindeodella prioniodon* Huddle ; Cooper : 614, Pl. 84, fig. 12.
 1945 *Metaprimiodus biangulatus* Huddle ; Cooper : 614, Pl. 84, figs. 13, 14.
 1947 *Hindeodella aculeata* ? Huddle ; Youngquist & Petersen : 244, Pl. 38, fig. 9.
 1947 *Hindeodella aculeata* Huddle ; Bond : 28, Pl. 1, figs. 19, 21.
 1947 *Hindeodella alternata* Ulrich & Bassler ; Bond : 29, Pl. 1, fig. 23.
 1947 *Hindeodella germana* Holmes ; Bond : 29, Pl. 1, fig. 22.
 1947 *Hindeodella germana* Holmes ; Bond : 29, Pl. 1, fig. 22.
 1947 *Hindeodella subtilis* Ulrich & Bassler ; Bond : 29, Pl. 1, fig. 25.
 1947 *Hindeodella* sp. 1 Bond : 29, Pl. 1, fig. 24.
 1947 *Hindeodella* sp. 2 Bond : 29, Pl. 1, fig. 20.
 1955 *Hindeodella germana* Holmes ; Sannemann : 130, Pl. 2, fig. 45.
 1955 *Hindeodella deflecta* Hibbard ; Sannemann : 129, Pl. s, fig. 6, Pl. 5, fig. 8.
 1957 *Hindeodella germana* Holmes ; Lys, Serre & Deroo : 800, Pl. 8, fig. 7.
 1957 *Hindeodella deflecta* Hibbard ; Lys, Serre & Deroo : 800, Pl. 8, fig. 6.

- 1959 *Hindeodella deflecta* Hibbard ; Helms : Pl. 4, fig. 32, Pl. 1, fig. 17.
 1960 *Hindeodella germana* Holmes ; Zimmermann : Pl. 1, fig. 16.
 1960 *Hindeodella germana* Holmes ; Dvorak & Freyer : Pl. 1, fig. 1.
 1961 *Hindeodella germana* Holmes ; Büdurov : 262, Pl. 3, fig. 11.
 1962 *Hindeodella germana* Holmes ; Spasov & Stevanovic : 58, Pl. 1, fig. 12.
 1962 *Hindeodella* sp. Winder : 91, fig. 1, 6.
 1965 *Hindeodella germana* Holmes ; Spasov : 86, 87, Pl. 1, fig. 10.
 1965 *Hindeodella similis* Ulrich & Bassler ; Spasov : 87, Pl. 1, fig. 11.

MATERIAL. 200 specimens : figured, X 180, X 177, X 178, X 179.

RANGE. North Crop KL 1-ZL 19, Avon Gorge K 3-Z 38.

DESCRIPTION. The main denticle is fairly massive, laterally compressed, biconvex in cross-section, recurved and posteriorly inclined. The anterior lateral process is curved inwards at an angle ranging from just a few degrees to nearly 90°. The considerably laterally compressed anterior lateral process is finely denticulate, often with the largest denticles at the anterior. The posterior bar is very thin, comparatively deep, and somewhat arched in some specimens, bearing fine, discrete, pointed denticles. The dentition tends to be cyclic, two major denticles being separated by three to four minute denticles, all more or less posteriorly inclined. There are up to 14 major denticles on the posterior bar. The posterior termination is composed of flat lying denticles, inclined at a low angle to the horizontal. It may be aborally convex ("upswept") in young forms.

The basal cavity is small, fairly deep, and situated at the anterior end of the apical denticle.

REMARKS. Throughout the Middle and Upper Devonian, and the Tournaisian and Viséan, there occurs a simple hindeodellid with a curved anterior lateral process. Many different authors have assigned different names to these hindeodellids, depending on minor variations in such features as the amount of deflection. Within our collections all types of deflection and various types of dentition can be seen to intergrade, and it is probable that all these forms belong to the same variable species. Further work may show that some of these characteristics may be of specific importance, but at the present time none can be separated.

Hindeodella tenuis Clarke

Plate 28, fig. 27

- 1900 *Ctenognathus obliquus* Hinde (*partim*) : 344, Pl. 10, fig. 38.
 1928 *Hindeodella obliqua* Holmes (*partim*) : 12, Pl. 5, fig. 5.
 1960 *Hindeodella tenuis* Clarke : 8, 9, Pl. 1, figs. 10, 11.

MATERIAL. 4 specimens : figured, X 187.

RANGE. North Crop 3D 12-14/15.

DESCRIPTION. The present specimens are similar to those described by Clarke. The posterior bar is elongated, deep, and decreases relatively little in depth towards its posterior end. The anterior two-thirds is straight and the posterior third gently down-flexed. The denticles tend to increase in size posteriorly, the most posterior

being both the largest and the most steeply inclined. The anterior fang is two to three times the basal width of the largest of the posterior denticles, and is slightly recurved. The anterior bar is relatively short and the denticles stand erect. The larger denticles of the posterior bar are separated by only 1 or 2 smaller denticles. The anterior lateral process is not strongly inflexed.

Hindeodella undata Branson & Mehl

Plate 31, fig. 1

- 1941 *Hindeodella undata* Branson & Mehl : 169, Pl. 5, fig. 3.
 1941 *Hindeodella* sp. Branson & Mehl : 170, Pl. 5, fig. 9.
 1953 *Hindeodella undata* Branson & Mehl ; Hass : 82, Pl. 16, figs. 5-7.
 1956 *Hindeodella undata* Branson & Mehl ; Elias : 108, Pl. 1, figs. 2, 10.
 1956 *Hamulosodina bransoni* Elias : 108, Pl. 1, fig. 4.
 1956 *Hamulosodina hassi* Elias : 108, Pl. 1, figs. 11, 12.
 1961 *Hindeodella undata* Branson & Mehl ; Higgins : Pl. 12, figs. 10, 12.
 1963 *Hindeodella undata* Branson & Mehl ; Bouckaert & Higgins : 17, text-fig. 3.
Hindeodella undata Branson & Mehl ; Collinson & Druce in press, text-fig. 10.

MATERIAL. 35 specimens : figured, X 185.

RANGE. North Crop 3D 4-3D 22.

DESCRIPTION. Specimens of this species are characterized by a relatively long, deep and straight posterior bar, the aboral margin of which is straight and sharp, and the sides relatively flat. The oral surface bears a series of alternating denticles which are acicular in general form, and discrete for the whole of their length. They taper sharply to a point. Larger denticles tend to be separated by groups of 2 or 3 smaller ones, which may be laterally offset from the denticles of the main series. The anterior fang is not greatly larger than the largest of the denticles of the posterior bar. It makes almost a right angle with the line of the posterior bar and is straight for the greater part of its length. The anterior inner lateral process is short and continuously inflexed. It bears one or more needle-like denticles on its oral edge.

Hindeodella sp.

Plate 29, figs. 12a, c

MATERIAL. 1 specimen : figured, X 445.

RANGE. North Crop ZLA 33.

DESCRIPTION. A single specimen of a small distinctive hindeodellid is illustrated. The posterior bar is short and relatively deep and bears a series of 5 denticles which increase in size posteriorly. The inclination of the 4 most posterior is about 45° to the line of the posterior bar, but the most posterior denticle is more strongly inclined. The apical denticle is rounded in cross-section and the lower part is more or less erect. The anterior process is sharply down-flexed and continuously inflexed, so that its distal end makes an angle of about 45° with the posterior bar. There is a well-developed, elongated basal cavity below the fang and the proximal part of the anterior aboral process.

Hindeodella sp. nov.

Plate 28, figs. 14a, b

MATERIAL. 1 specimen : X 186 (figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample 3D 14/15.

DESCRIPTION. A single specimen is tentatively regarded as a new species of *Hindeodella*, although it may be a pathologic form. It is characterized by a continuously recurved, hooked anterior lateral process and a very sinuous posterior bar. The general appearance of the unit is of a question mark, with the posterior end forming the base of the question mark. The posterior bar is shallow, being about equal in depth to the smaller series of denticles developed on its oral surface. Its aboral edge is strongly convex in its anterior half and concave in its posterior half, so that the whole effect is of a sinuous development. Its outer lateral face is strongly convex in the anterior half, and flat to gently convex in the posterior part.

The oral surface of the posterior bar bears a series of about 18 denticles of variable size, which show no regular alternation. They are basally confluent but apically distinct, and are sharply pointed, with sharp anterior and posterior edges. Those near the posterior end tend to be more strongly inclined posteriorly than those in the anterior part, which are only gently inclined posteriorly. Although these denticles show no regular alternating arrangement, some of them are conspicuously larger than others and these are developed at variable intervals. The largest of them are about twice the length of the smallest, and they show a broad tendency to increase in size posteriorly. Their total number is probably greater than 18 as the present specimen is broken. The main denticle is about equal in size to the largest denticles of the posterior bar, being sharply recurved and incurved. Immediately posterior to it the aboral surface of the posterior bar is flat, although its general structure is still broadly convex.

The antero-lateral process consists of two more or less distinct parts. There is a sharply up-flexed part, in which the aboral edge of the process makes an angle of about 70° with the aboral edge of the posterior bar immediately posterior to the main denticle. It is not greatly flexed to the natural plane, however. On the anterior end of this are two conspicuous denticles, which are incurved, as well as recurved, so that their "anterior and posterior" edges are in fact lateral in position. They are greater in size than the main denticle and exceed the size of the largest denticles of the posterior bar by about a half. The aboral surface of the unit is excavated by a very thin groove.

Genus *HINDEODUS* Rexroad & Furnish 19641964 *Hindeodus* Rexroad & Furnish : 671TYPE SPECIES. *Trichonodella imperfecta* Rexroad.

Hindeodus alatoides (Rexroad & Burton)

Plate 31, figs. 7, 10.

- 1961 *Falcodus* ? *alatoides* Rexroad & Burton : 1152, Pl. 140, fig. 8.
 1964 *Hindeodus alatoides* (Rexroad & Burton) Rexroad & Furnish : 67, Pl. 111, figs. 18, 19.
 1961 *Falcodus* (?) n. sp. Rexroad & Collinson : Pl. 1.
 1965 *Hindeodus alatoides* (Rexroad & Burton) Rexroad & Nicoll : 20, Pl. 2, fig. 10.

MATERIAL. 3 specimens : figured, X 193, X 192.

RANGE. Scotland HOSIE 2B-2C.

DESCRIPTION. The present specimens are distinguished by the short laterally flexed anterior limb, which is deepest and bears the largest denticles distally. The apical denticle is only slightly inclined posteriorly and its distal portion is straight. It is little compressed laterally. The posterior bar is straight and elongated, its length being about three times that of the anterior bar. The denticles are short, discrete and bluntly pointed, tending to alternate in size and standing more or less erect to the posterior bar in some specimens, but being slightly inclined in others. The apical denticle is conspicuously elongated, and has a basal width of up to three times that of the adjacent denticles. The denticles of the posterior bar tend to increase in size posteriorly. The aboral cavity is relatively small.

Hindeodus imperfectus (Rexroad)

Plate 31, fig. 8

- 1957 *Trichonodella imperfecta* Rexroad : 41, Pl. 4, figs. 4, 5.
 1958 *Trichonodella imperfecta* Rexroad ; Rexroad : 26, Pl. 4, fig. 6.
 1961 *Elsonella* ? *imperfecta* (Rexroad) Rexroad & Collinson : 6.
 1961 *Elsonella* ? *imperfecta* (Rexroad) Rexroad & Burton : 1152, Pl. 141, fig. 1.
 1964 *Hindeodus imperfectus* (Rexroad) Rexroad & Furnish : 672, Pl. 111, figs. 13, 14.
 1965 *Hindeodus imperfectus* (Rexroad) Rexroad & Nicoll : 20, Pl. 2, fig. 11.

MATERIAL. 1 specimen : figured, X 194.

RANGE. Scotland HOSIE 2B.

DESCRIPTION. The present specimens are generally fragmentary, but they show

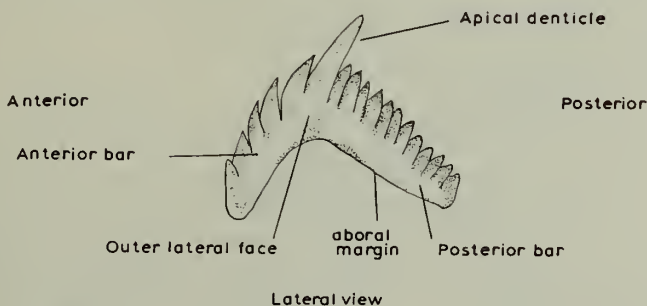


FIG. 25. *Hindeodus* sp. showing morphological terms used in the text.

the general symmetry of this species, a feature that is so striking that it led Rexroad in his initial description to assign it to the genus *Trichonodella*. The denticles tend to increase in size towards the distal third of the bars, and the apical denticle tends to stand erect between the converging denticles of the anterior and posterior bars. There is a feeble basal flange below the apical denticle.

Hindeodus sp.

Plate 22, figs. 17a-20b

1964 *Hindeodus* sp. Rexroad & Furnish : 672, Pl. 111, fig. 11.

MATERIAL. 10 specimens : figured, X 189, X 191, X 188, X 190.

RANGE. Scotland HOSIE 2A-2B.

DESCRIPTION. Certain of the present specimens, although showing minor variations in form, are obviously closely related to one another. These specimens possess a short, deep, posterior bar which has a straight aboral margin in lateral view. The bar is slightly flexed inwards longitudinally and its oral surface bears at least 10 confluent denticles, only their apices being discrete and bluntly pointed. They are inclined gently posteriorly and are more or less of uniform size. The apical denticle is about twice as long as the largest denticles of the rest of the bar. It is basally confluent to those on either side of it and has sharp anterior and posterior edges and a strongly biconvex cross-section. The anterior bar is shorter than the posterior, and is gently concave basally in lateral view. Its oral surface bears a series of about 5 denticles, similar in form to those of the posterior bar, which tend to decrease in size anteriorly and which are recurved so that they lie sub-parallel to the apical denticle. It makes an angle of about 90° - 110° with the posterior bar. The denticles of the anterior bar tend on the whole to be rather broader than those of the posterior. The inner lateral face of the anterior bar is gently concave. In outer lateral view the whole unit is seen to be gently arched inwardly and its outer lateral face is flat to gently convex. There is a slightly expanded cavity below the apical denticle and very fine longitudinal grooves extend along the lengths of the two bars.

Genus *KLADOGNATHUS* Rexroad 1958

1958 *Kladognathus* Rexroad : 19 (*pro Cladognathus* Rexroad 1957, 28 *non* Burmeister 1847).

1961 *Cladognathodus* Rexroad & Collinson : 6 (abs. syn.).

TYPE SPECIES. *Cladognathus prima* Rexroad.

This genus was first described by Rexroad in 1957 under the name *Cladognathus*, a name later found to be a homonym of one used by Burmeister in 1847. The name *Kladognathus* was proposed by Rexroad 1958, as a substitute. Rexroad & Collinson (1961 : 6), however, changed this to *Cladognathodus* because they suggested that the replacement of a letter "C" by a letter "K" did not represent a valid name change under the rules of nomenclature. Article 56A of the International Code makes it clear, however, that a difference of even one letter in the spelling of generic names represents a valid distinction between them. The name *Kladognathus* Rexroad 1958

is thus the senior and correct name for the genus, and *Cladognathodus* Rexroad & Collinson 1961 is a junior synonym. We are grateful to Dr. Curt Teichert for pointing this out to us (see also Mound 1965).

Kladognathus clarensis Collinson & Druce

Plate 23, figs. 1a-2b

Kladognathus clarensis Collinson & Druce (in press).

MATERIAL. 3 specimens : figured, X 195, X 196.

RANGE. North Crop 3D 10-3D 23.

DESCRIPTION. In lateral view this species resembles the genus *Metalonchodina*. Its most striking feature is the greatly enlarged, laterally compressed denticle which comprises most of the posterior bar. This is inclined posteriorly but the curvature may be more or less continuous, or it may be chiefly confined to the base, with the upper part of the denticle having straight anterior and posterior edges. The inner lateral face tends to be rather more convex than the outer. The posterior aboral termination is more or less sharply pointed.

The fang is relatively small in comparison with the posterior denticle. It is slender, posteriorly continuously recurved, and has sharp anterior and posterior edges. The anterior bar consists of 1 to 3 denticles and the anterior aboral margin is spatulate in form with the anterior aboral angle being rounded. In multidenticulate anterior bars the most anterior denticles tend to be more or less erect, but the more posterior ones tend to be recurved.

The lateral process is short and bears at least one oral denticle. The whole unit tends to be laterally deflected, the outer lateral face tending to be concave. The aboral surface below the main denticle on the posterior bar is broad, and has a conspicuous flattened basal surface. It consists essentially of an inverted basal cavity, with a median groove which is continued along the anterior bar. All of the three present specimens have a short, laterally compressed, inconspicuous denticle lying between the fang and the main denticle of the posterior bar.

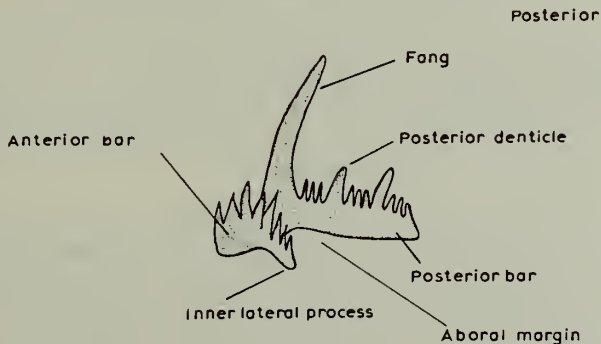


FIG. 26. *Kladognathus* sp. showing morphological terms used in the text.

REMARKS. The present specimens show strong resemblances to those described by Clarke (1960) as *Ligonodina complectens*. Rexroad & Collinson (1963 : 13) transferred Clarke's specimens to the genus *Magnilaterella*. The present specimens differ from those of Clarke chiefly in the presence of an anterior bar, and it is this distinctive feature which justifies their inclusion in the genus *Kladognathus*.

***Kladognathus macrodentatus* (Higgins)**

Plate 23, figs. 3-6

- 1961 *Lambdagnathus macrodentata* Higgins : 214, Pl. 12, figs. 1-3, text-fig. 3.
 1963 *Lambdagnathus macrodentata* Higgins ; Bouckaert & Higgins : 17, fig. 3.
Kladognathus macrodentata (Higgins) Collinson & Druce (in press).

MATERIAL. 15 specimens : figured, X 197, X 198, X 199, X 200.

RANGE. North Crop 3D 10-3D 22.

DESCRIPTION. This species is characterized by a long arched posterior bar which bears characteristically hindeodellid denticulation on its oral surface. The larger denticles are separated by 1 or 2 smaller denticles, which are basally confluent but apically discrete. In well preserved specimens the major denticles of the series are very long, the largest, in the middle of the posterior blade, commonly being about three times the depth of the posterior bar.

The short laterally compressed anterior bar is downflexed, but lies in the same plane as the posterior bar. Its anterior aboral margin is bluntly spatulate. There tend to be 2 or 3 small denticles in front of the apical denticle. The lateral bar is short, deeply arched, laterally compressed, and strongly deflected posteriorly, making an angle of 25°-45° with the arcuate posterior bar when seen in oral view. The lateral bar carries 1 or 2 stout, discrete denticles on its oral surface. The aboral margin of the entire unit is excavated by a shallow groove.

***Kladognathus mehli* (Rexroad)**

Plate 31, fig. 15

- 1957 *Cladognathus mehli* Rexroad : 29, Pl. 1, figs. 11, 12.
 1958 *Kladognathus mehli* (Rexroad) Rexroad : 19, Pl. 3, fig. 5.
 1965 *Kladognathus mehli* (Rexroad) Rexroad & Nicoll : 20, 21, Pl. 1, fig. 7.

MATERIAL. 3 specimens : figured, X524.

RANGE. North Crop 3D 14/15.

DESCRIPTION. This species is characterized by a very large, laterally compressed recurved fang, strong discrete denticles on the anterior and posterior bars, relatively strong curvature on the anterior and posterior bars, and a conspicuous attachment scar on the inner lateral face at the anterior end of the posterior bars. Our specimens agree closely with those illustrated by Rexroad.

Genus *LIGONODINA* Ulrich & Bassler 1926

- 1925 *Ligonodina* Bassler : 218 (*nom. nud.*).
 1926 *Ligonodina* Ulrich & Bassler : 12, 13.

TYPE SPECIES. *Ligonodina pectinata* Ulrich & Bassler 1926.

Ligonodina beata nom. nov.

Plate 26, figs. 4-6b

- 1934 *Ligonodina delicata* Branson & Mehl : 199, Pl. 14, figs. 22, 23.
 1934 *Ligonodina delicata* Branson & Mehl ; E. R. Branson : 328, Pl. 27, fig. 3.
 1934 *Ligonodina* sp. Huddle : 62, Pl. 12, fig. 8.
 1939 *Ligonodina delicatula* Cooper : 390, Pl. 45, figs. 50, 60, 61.
 1943 *Ligonodina tenera* Cooper & Sloss : 174, Pl. 29, fig. 34.
 1944 *Ligonodina delicata* Branson & Mehl ; Branson & Mehl *in* Shimer & Shrock : 241, Pl. 93, fig. 74.
 non 1944 *Ligonodina delicata* Branson & Mehl ; E. B. Branson : Pl. 26, fig. 23, (= *Palmatolepis* sp.).
 1947 *Ligonodina delicata* Branson & Mehl ; Miller & Youngquist : 509, 510, Pl. 73, fig. 12.
 1949 *Ligonodina delicata* Branson & Mehl ; Thomas : 408, 411, Pl. 4, fig. 22.
 non 1949 *Ligonodina delicata* ? Branson & Mehl ; Thomas : Pl. 3, fig. 41, (= *Ligonodina* sp.).
 non 1964 *Ligonodina delicata* Branson & Mehl ; Bergström : 28, text-fig. 12. Bergström (1964, 28) has demonstrated that *Phragmodus delicatus* Branson & Mehl, 1933, 123, Pl. 10, fig. 22) should be regarded as a species of *Ligonodina*. The name for this species, therefore, has precedence over that of *Ligonodina delicata* Branson & Mehl (1934, 199) and the latter species becomes a junior homonym of the former. In this case, it is necessary to select a new name, and we have selected the name *Ligonodina beata*. The holotype is University of Missouri Catalogue No. C. 243-4 (Branson & Mehl 1934 : 199).
 non 1964 *Ligonodina delicata* Branson & Mehl ; Budurov & Tschurner : Pl. V, figs. 23a, b.

MATERIAL. 361 specimens : figured, X 202, X 203, X 201.

RANGE. North Crop KL 19-ZLA 21, Avon Gorge K 3-C 25.

DESCRIPTION. A fragile unit with a slender main denticle which has a sub-circular cross-section. The main denticle is recurved posteriorly at 45°. The anterior-aboral process originates immediately anterior to the main denticle, and commonly bears 3 or 4 isolated, discrete, sub-circular denticles, which are posteriorly inclined. The posterior bar is fairly long and rarely preserved. It bears up to 6 isolated laterally compressed denticles, which are posteriorly inclined, and tend to increase in size posteriorly.

In aboral view, the anterior portion of the posterior bar is excavated, the deepest excavation being beneath the main denticle ; the cavity extends inverted beneath the anterior aboral process. The cavity is grooved, the groove running some way along the posterior bar and the complete length of the anterior aboral process.

REMARKS. Our specimens agree very closely to the holotype described by Branson & Mehl.

Ligonodina levis Branson & Mehl

Plate 26, figs. 15a, b, 17a-19b

- 1941 *Ligonodina levis* Branson & Mehl : 185, Pl. 6, fig. 10.
 1949 *Ligonodina* sp. Youngquist & Miller (*partim*) : 620, Pl. 101, figs. 12 & 13 only.
 1957 *Ligonodina levis* Branson & Mehl ; Bischoff : 30, Pl. 5, figs. 8, 9, Pl. 6, fig. 25.
 1957 *Ligonodina obunca* Rexroad : 32, Pl. 1, figs. 22, 23.
 1958 *Ligonodina obunca* Rexroad ; Rexroad : 21, Pl. 3, figs. 7, 8.
 1961 *Ligonodina levis* Branson & Mehl ; Rexroad & Burton : 1154, Pl. 141, figs. 7, 8.
 1963 *Ligonodina levis* Branson & Mehl ; Thompson & Goebel : 11, fig. 3.
 1963 *Ligonodina levis* Branson & Mehl ; Rexroad & Collinson : 11, Pl. 2, figs. 24, 25.
 1964 *Ligonodina levis* Branson & Mehl ; Rexroad & Furnish : 672, Pl. 111, fig. 381.
 1965 *Ligonodina levis* Branson & Mehl ; Rexroad & Nicoll : 21, Pl. 2, fig. 24.

MATERIAL. 25 specimens : figured, X 204, X 205, X 206, X 207.

RANGE. North Crop CYD 6-3D 14/15, Avon Gorge Z 38-D 26.

DESCRIPTION. Rexroad's original description of this particular species was rather generalized, but the distinctive features seem to be the massive and rather rounded main denticle, which is continuously recurved, especially in its lower part, so that its distal portion makes an angle of about 45° with the posterior bar. The distal portion is not greatly laterally compressed, although it has sharp anterior and posterior edges ; the lateral faces are themselves strongly convex. The posterior edges become obsolescent towards the proximal end. The outer lateral aboral surface is expanded slightly laterally, but has a conspicuous flange-like structure developed along it, which slopes towards the aboral cavity. The proximal inner portion of the main denticle is very strongly convex.

The posterior bar is of unknown length but is more or less quadrate in cross-section, with a broad aboral edge. It bears at least one, stump-like denticle, which is well separated from the base of the main denticle. The antero-aboral surface of the main denticle tends to be rather rounded, and in oral-outer lateral view extends below the main level of the denticle in a rather bluntly pointed termination. The main denticle extends in a continuous curve downward to form the inner anterior aboral process. The aboral surface of this process lies at an acute angle, often as small as 45° , to the posterior bar. Its oral surface bears up to 5 large denticles, of which those at the anterior end tend to be very large. They are straight to slightly curved

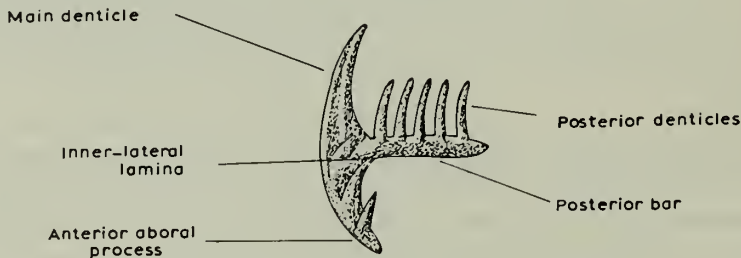


FIG. 27. *Ligonodina* sp. showing morphological terms used in the text.

and are directed inwards and upwards. The denticles are discrete and more or less sub-circular in cross-section.

The antero-aboral process decreases in thickness towards the distal end. The aboral surface is characterized by thick, aborally directed, lip-like, flange structures along the lateral edges of both the posterior bar and the antero-aboral process. There is a pit-like cavity below the main denticle and there are longitudinal grooves along the aboral surface of the posterior bar and the antero-aboral process. These decrease in width towards the distal end of the process.

Ligonodina magnilaterina sp. nov.

Plate 26, figs. 8a-11b

DERIVATION OF NAME. From the resemblance of the species to the genus *Magnilaterella*.

DIAGNOSIS. Ligonodinid with a denticle situated anterior to main denticle, forming continuation of denticle series of posterior bar. Anterior denticle only slightly smaller in size than main denticle, though tending to be rather more slender in general form ; lying at junction of antero-aboral process and posterior bar.

MATERIAL. 6 specimens : Holotype X 211, Paratypes (all figured) X 208, X 209, X 210.

TYPE LOCALITY AND HORIZON. Scotland Sample HOSIE 2C.

RANGE. Scotland HOSIE 2C.

DESCRIPTION. The main denticle is strong, the base being strongly developed anteriorly and posteriorly. It is of unknown length, sub-circular in cross-section in the lower part. The main denticle is recurved in its lower part, the inner and outer lateral faces being strongly convex. The posterior margin of the main denticle is extended to form the oral surface of the posterior bar. This bar is of unknown length, but is deep in its anterior part and bears at least 4 discrete denticles, which are only slightly laterally compressed and of variable size. It is possible that they may be arranged in a cyclic pattern.

On the anterior face of the main denticle a thickened denticle is developed at the junction of the anterior denticle and the antero-aboral process. This denticle is distinct from those of the antero-aboral process and in inner lateral view it seems to represent a continuation of the posterior bar. In outer lateral view it may be seen to be recurved inwardly at its base ; its anterior face is strongly convex with sharp lateral edges. It is recurved slightly posteriorly to lie sub-parallel to the main denticle, and also slightly inwardly. It is fused at the base to the main denticle and arises from it at a strongly convex junction. It is long and slender, being sharply pointed at its distal end and is about half the diameter of the main denticle. The other denticles of the anterior aboral process, which number at least three, are discrete, sub-circular in cross-section with poorly defined, but rather sharp, lateral edges. They tend to decrease in size distally. The anterior aboral process appears to be relatively short, although none of the present specimens is complete. It is

strongly recurved in a vertical plane and its proximal aboral surface makes almost a right angle with the posterior bar. It is also strongly recurved with respect to the aboral surface of the posterior bar. The curvature of the anterior edge of the process is in line with the anterior denticle and not with that of the main denticle. It makes an angle of about 45° with the posterior bar in a horizontal plane.

The aboral surface is excavated by a very shallow and rather inconspicuous groove, which runs along at least the anterior part of the posterior bar and is continuous with a similar cavity below the anterior aboral process. The cavity below the main denticle is very narrow and not over-deep.

REMARKS. This species is distinguished from all other ligonodinids by the form and the position of the denticle anterior to the main denticle. In this feature it approaches, but does not reach, the typical forms of the genus *Magnilaterella* Rexroad and it is also reminiscent to some extent of some Ordovician species of the genus *Phragmodus*.

Ligonodina osborni sp. nov.

Plate 26, figs. 1a-2c

DERIVATION OF NAME. This species is named in honour of Mr. S. Osborn of the Geology Department, University College of Swansea.

DIAGNOSIS. Ligonodinid with a conspicuous continuously recurved main denticle, strongly biconvex in cross-section, with feeble anterior and posterior edges, distal portion not preserved in present specimens. Posterior bar of unknown length, strongly depressed in vertical plane, bearing on oral surface series of isolated, posteriorly inclined denticles, appearing to increase in size posteriorly; separated by distance about equal to their basal width. A short, sinuous, sharply flexed, pointed anterior aboral process, bearing 2 isolated denticles; proximal larger than distal.

MATERIAL. 6 specimens: Holotype X 212, Paratype X 213 (both figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample 3D 14/15.

RANGE. North Crop 3D 8-3D 14/15.

DESCRIPTION. The main denticle is large and strongly recurved, its whole anterior edge being strongly convex, and its posterior strongly concave. The distal portion is of unknown form but the basal part is biconvex in outline, with only inconspicuously developed anterior and posterior edges. It is extended posteriorly into a strongly arched posterior bar, the aboral edge of which is concave. Its lateral faces are flat or only very feebly convex, and there is a sharp basal ledge developed along its preserved length. Its oral surface bears at least 3 isolated, posteriorly inclined, denticles, which are biconvex in cross-section, and the third of which is larger than the first or second. These are inclined at an angle of about 45° to the posterior bar, and are separated by a distance about equal to their basal width.

The antero-aboral process makes an angle in a vertical plane of about 90° with the line of the posterior denticle, so that its denticles point directly inwards and also a little posteriorly, because of their recurvature. It bears at least 2 isolated denticles,

which are biconvex in cross-section and have inconspicuous lateral edges. They are separated by a great distance and the distal is the smaller of the two. The whole anterior aboral surface tapers rapidly towards its distal tip; although its depth remains constant, its width decreases conspicuously. Its distal tip is also flexed gently forward. In lateral view the most striking feature of the anterior aboral process is that it is so recurved posteriorly that it has an angular protruding junction with the base of the main denticle. It is then flexed forwards so that the whole appearance of the combined aboral process and anterior denticle is of a feebly sinuous line. In outer lateral view the flexure and decrease in width of the anterior aboral process are conspicuous features. The lip below the main denticle is also strikingly developed in lateral view, the whole inner lateral face of the unit being very feebly convex. In aboral view the unit is greatly expanded below the main denticle and there is a conspicuously flattened, but sloping, surface which is deeper on the outer lateral side. It narrows rapidly towards the posterior bar, which is excavated by a relatively deep, rounded groove. The main basal cavity is restricted to the median part below the main denticle. The anterior aboral process also has a very wide aboral surface, which is only partly excavated, but it narrows rapidly towards a pointed distal end and is somewhat twisted in aboral view. It is deflected to make an angle of 90° in a vertical plane with the main denticle.

Ligonodina roundyi Hass

Plate 26, figs. 13a-14b, 16a-c

- 1926 *Prioniodus* sp. A. Roundy : 11, Pl. 4, fig. 9.
 1926 *Prioniodus* sp. C. Roundy : 11, Pl. 4, fig. 11.
 1953 *Ligonodina roundyi* Hass : 82-83, Pl. 15, figs. 5-9.
 1956 *Ligonodina roundyi* Hass : Elias : 126, Pl. V, figs. 10-14.
 1958 *Ligonodina roundyi* Hass ; Rexroad : 21, Pl. 3, figs. 1-4.
 1961 ?*Ligonodina typha* (Gunnell) Higgins : 220, Pl. 11, fig. 6.
Ligonodina roundyi Hass ; Collinson & Druce (in press).

MATERIAL. 24 specimens : figured, X 214, X 215, X 216.

RANGE. North Crop 3D 14/15.

DESCRIPTION. This species of *Ligonodina* is characterized by a massive and elongate main denticle and a strongly developed antero-aboral process. The posterior bar is relatively slender in comparison with the proportions of the two latter elements.

The main denticle is greatly elongated, and more or less strongly expanded anteriorly and posteriorly at its base. It is sharply pointed and in its distal half it is very strongly laterally compressed, the anterior and posterior edges being sharp and the lateral faces feebly convex. The curvature of the main denticle is concentrated in the proximal third, the remainder being straight. It is also twisted in the vertical plane, so that the anterior edge points inwardly; in its outer aboral portion the main denticle is strongly rounded, but the corresponding inner lateral face is flat to feebly concave. Along the inner anterior margin a relatively strong and sharp keel is

developed, which is the main anterior edge of the denticle ; it extends aborally as a sharp ridge, which forms the edges of the denticles of the anterior aboral process. The posterior face of the main denticle tends to become rather depressed and may develop a low concave depression.

The antero-aboral process points vertically downwards, making an angle of 80° – 100° with the posterior bar. It is not deflected out of line with the main denticle to any great extent. The oral surface of the anterior aboral process bears up to 6 denticles, the largest of which occurs in the medial portion ; the denticles are strongly compressed anteriorly and posteriorly in their distal portions. Though their bases are sub-circular in outline, they have strong lateral edges and are recurved inward and upward ; they are discrete but relatively closely spaced. The posterior bar is relatively slender and bears at least 2 (the present specimens are all broken) discrete, sub-circular, widely spaced, feebly posteriorly inclined, bluntly pointed, peg-like denticles.

The outer lateral face of the main denticle is strongly flared and the edges of the cavity are thick ; there is a deep, but limited lip below the main denticle which is extended along the aboral anterior process as a conspicuous longitudinal groove on the aboral surface ; it is also extended for at least some distance along the posterior bar.

The width and depth on the antero-aboral process decrease towards the distal extremity, which is bluntly rounded. The posterior bar is more or less quadrate in cross-section.

Ligonodina tenuis Branson & Mehl

Plate 31, figs. 4, 16

- 1941 *Ligonodina tenuis* Branson & Mehl : 170, Pl. 5, figs. 13, 14.
 1949 *Ligonodina* sp. Youngquist & Miller (*partim*) : 620, Pl. 101, fig. 11 only.
 1956 *Ligonodina tenuis* Branson & Mehl ; Elias : 126, Pl. 5, figs. 4, 5.
 1957 *Ligonodina* sp. Rexroad : 33, Pl. 1, figs. 20, 21.
 1957 *Ligonodina hamata* Rexroad : 32, Pl. 1, figs. 24, 25.
 1958 *Ligonodina hamata* Rexroad ; Rexroad : 21, Pl. 3, figs. 9–14.
 1960 *Ligonodina tulensis* (Pander) Clarke 11, Pl. 2, fig. 4.
 1961 *Ligonodina obunca* Rexroad ; Higgins : Pl. 11, fig. 9.
 1961 *Ligonodina hamata* Rexroad ; Rexroad & Burton : 1154, Pl. 141, figs. 5, 6.
 1964 *Ligonodina tenuis* Branson & Mehl ; Rexroad & Furnish : 672, Pl. 111, fig. 40.
 1965 *Ligonodina tenuis* Branson & Mehl ; Rexroad & Nicoll : 22, Pl. 2, figs. 12–15.

MATERIAL. 15 specimens : figured, X 320, X 321.

RANGE. North Crop 3D 8–3D 22.

DESCRIPTION. Specimens of the species, though generally fragmentary, display the distinctive features of the holotype. They have a characteristically strongly developed long, slender main denticle, which is continuously recurved, although the distal portion tends to be rather straight : the lateral faces are convex to flat, and the aboral margin tends to bear a more or less conspicuous ledge. The denticles of the posterior bar are relatively small in comparison with the size of the unit.

Ligonodina tulensis (Pander)

Plate 31, fig. 9

- 1856 *Prioniodus tulensis* Pander (*partim*) : 30, tab. 2a, fig. 19 only.
 1900 *Prioniodus tulensis* Pander ; Hinde (*partim*) : 343, Pl. 9, fig. 15 only.
 1928 *Prioniodus tulensis* Pander ; Holmes (*partim*) : 22, Pl. 3, fig. 22 only.

MATERIAL. 6 specimens : figured X 328.

RANGE. North Crop CYD 6-CYD 7.

DESCRIPTION. The present specimens are fragmentary but they display most of the features described by Clarke. The main denticle tends to be rather large in comparison with the size of the posterior bar ; its lateral faces are flat to gently convex, and in its lower portion the anterior and posterior edges tend to be blunted. The denticles of the posterior bar are relatively small, and are discrete. The anterior aboral process is strongly recurved laterally, and is also twisted, so that the denticles are directed anteriorly. Its distal end makes a right angle in a horizontal plane with the posterior bar. The denticles of the process tend to be rather larger than those of the posterior bar.

Ligonodina sp. A

Plate 26, figs. 3a-c

MATERIAL. 10 specimens : figured, X 217.

RANGE. North Crop ZLA 32-ZLA 33.

DESCRIPTION. All the present specimens are broken, but the species appears to be a ligonodinid with a greatly excavated main denticle. The main denticle itself is massive, sub-circular in cross-section, with a sharp lateral costa developed in line with the anterior aboral process. The antero-aboral process is broken, but the posterior bar can be seen to be short, bearing three tall isolated denticles, and having its aboral side grooved.

REMARKS. The overall appearance of this species is of a *Roundya* with only one limb of the anterior arch developed. Youngquist, Miller & Downs (1950 : 527) illustrate and describe similar forms as *Ligonodina?* sp. Our material is too fragmentary for a specific designation but it would appear that the two forms may be conspecific.

Ligonodina ? sp.

Plate 26, fig. 7

MATERIAL. 1 specimen : figured, X 218.

RANGE. North Crop ZLA 11.

DESCRIPTION. This appears to be a pathological form of *L. beata*. There is a secondary lateral process developed on the inner side of the posterior bar and it bears one low node. The angle of the process, and its inclination toward the posterior, are parallel to that of the antero-aboral process. The basal cavity is extended along it on the aboral side.

Ligonodina ? sp.

Plate 26, figs. 12a-b

MATERIAL. 1 specimen : figured, X 219.

RANGE. North Crop 3D 10.

DESCRIPTION. This single specimen is presumably a pathological form of the genus *Ligonodina*. It is characterized by the presence of the antero-aboral process and by the fact that the main denticle can just be discerned when the lighting is favourable. On the posterior edge of this denticle, however, and continuous with it, there is a sheet-like development of conodont material which extends in the same plane as the posterior bar. Only the anterior denticle is visible within this by reflected light. The denticles of the antero-aboral process are sub-circular in form, 3 in number, and discrete, the middle one of the three being the largest. The form of the outer lateral face of the extension of the anterior denticle suggests that the conodont was attached by this surface ; this then became an aboral surface although in " normal " specimens it would have represented an upper lateral surface.

Genus *LONCHODINA* Ulrich & Bassler 19261925 *Lonchodina* Bassler : 219 (nom. nud.).1926 *Lonchodina* Ulrich & Bassler :TYPE SPECIES. *Lonchodina typicalis* Ulrich & Bassler 1926.*Lonchodina bolbosa* Collinson & Druce

Plate 24, figs. 12a-14b

1957 *Lonchodina nitela* Huddle ; Ziegler in Flügel & Ziegler : 44, Pl. 4, fig. 19.1961 *Lonchodina* cf. *projecta* (Ulrich & Bassler) Higgins ; 220, Pl. XI, fig. 10.*Lonchodina bolbosa* Collinson & Druce (in press).

MATERIAL. 12 specimens : figured, X 223, X 222, X 224.

RANGE. North Crop 3D 8-3D 14/15.

DESCRIPTION. The distinctive features of this species are the relatively sub-equal short and rather slender bars, the conspicuous basal flaring below the apical denticle on the outer lateral face and the divergence of the two bars below the denticle at an angle of more than 90° ; in some specimens the angle approaches a right angle, but in others, the angle may be as high as 110°.

The present specimens are very fragmentary but they show the long recurved, laterally compressed apical denticle, the distinctive flaring cavity, and the straight and relatively short anterior aboral process described by Collinson & Druce. The basal excavation below the main denticle is large but shallow, and is extended as a very narrow groove along the anterior aboral process.

Lonchodina furnishi Rexroad

Plate 24, figs. 20a-23c

- 1957 ?*Lonchodina subsymmetrica* Ulrich & Bassler ; Bischoff : Pl. 1, figs. 19, 21, 22.
 1958 *Lonchodina furnishi* Rexroad : 22, Pl. 4, figs. 11-13.
 1961 *Lonchodina furnishi* Rexroad ; Higgins : Pl. 11, fig. 3.
 non 1962 *Lonchodina furnishi* ? Rexroad ; Higgins : Pl. 1, fig. 4.
 1963 *Lonchodina furnishi* Rexroad ; Bouckaert & Higgins : 17, fig. 3.
Lonchodina furnishi Rexroad ; Collinson & Druce (in press).

MATERIAL. 5 specimens : figured, X 225, X 226, X 228, X 227.

RANGE. North Crop 3D 8-3D 19.

DESCRIPTION. The distinctive feature of this species is the more or less symmetrical development of the cavity below the apical denticle on both sides of the bar, rather than being restricted to only one side of it. The anterior bar is stout and deep increasing slightly in depth towards the anterior end. It bears about 5 stout denticles which are basally confluent but discrete for two thirds of their length. They tend to be sub-triangular in profile and to be sharply pointed, with sharp anterior and posterior edges and gently to strongly convex lateral faces. The curvature on the outer faces tends to be stronger than that on the inner, the denticles on the median third of the bar tending to be the largest. The anterior denticle is small and relatively inconspicuous. The apical denticle is about twice the length of the largest denticle of the anterior bar ; it is strongly posteriorly inclined rather than recurved, its edges being straight. It lies in approximately the same horizontal plane as the distal end of the anterior bar. Its inner lateral face is strongly convex at the base, becoming feebly convex in its upper surface ; its outer lateral face is rather more strongly convex. Throughout its length it is sharply pointed and is also directed inwardly as well as posteriorly. The outer lateral face of the anterior bar is feebly ridged longitudinally along its upper surface, about one third of its depth below the junction with the oral denticles ; below this point it slopes gently inwards and has a flat feebly concave surface. The bar itself is curved in a vertical plane and is also slightly deflected inwardly.

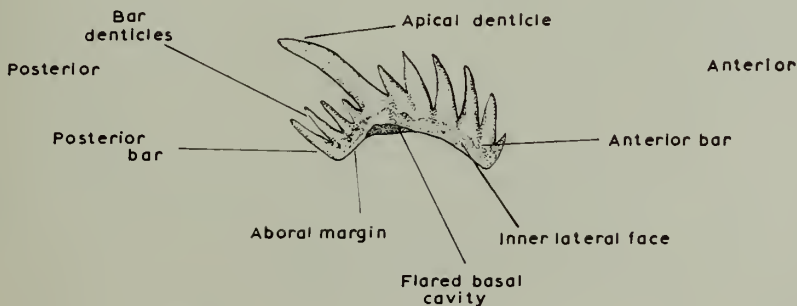


Fig. 28. *Lonchodina* sp. showing morphological terms used in the text.

The posterior bar is depressed, but is more or less straight ; it bears about 4 denticles which are discrete, sub-triangular in profile and sharply pointed, their bases being confluent ; they have sharp posterior and anterior edges, feebly convex lateral faces, and are inclined parallel to the apical denticle, though they are not recurved inwardly to the same extent. The posterior bar is more shallow and slender than any part of the anterior bar and is only about one third to a half the length of the latter.

Both bars are excavated by fine longitudinal grooves and there is a conspicuous flaring cavity below the apical denticle on both the inner and outer lateral faces of the unit, about which it is sub-symmetrical, though not symmetrical in detail, the inner lateral flaring occurring rather posterior to the outer lateral flaring.

REMARKS. The denticles on the anterior bar may number up to 8 in some specimens. The species shows some variation in the degree of lateral deflection of the bars in a horizontal plane. Some specimens (e.g. Pl. 24, fig. 23b) show the posterior bar considerably flexed outward as well as vertically.

Lonchodina obtunda Collinson & Druce

Plate 24, figs. 7a-c

- 1957 *Lonchodina projecta* (Ulrich & Bassler) Ziegler in Flügel & Ziegler : 44, Pl. 4, fig. 14
(non Pl. 5, fig. 12).
- 1962 ?*Lonchodina* cf. *projecta* (Ulrich & Bassler) Higgins : Pl. 1, fig. 5.
Lonchodina obtunda Collinson & Druce (in press).

MATERIAL. 5 specimens : figured, X 229.

RANGE. North Crop 3D 8-3D 17.

DESCRIPTION. The distinctive features of the species are the relatively delicate construction of the whole unit, the large sub-apical cavity which is developed on the inner lateral surface, and the very wide angle of divergence of the anterior and posterior bars, which in Collinson & Druce's type specimens is 110°-135°.

The present specimens are incomplete but they show a relatively slender anterior bar, with about 5 widely spaced though virtually basally confluent, denticles ; they are curved upward and inward and have biconvex lateral faces, the inner being the stronger, and relatively sharp edges. The denticles of the anterior bar range up to at least 5 in number. The apical denticle is strong and more or less sub-circular in cross-section, though it has prominent anterior and posterior edges in its proximal portions ; it is curved inwards and backwards, and its inner lateral face is very strongly expanded to give a wide flaring basal cavity which extends as a groove along the bars. The posterior bar is broken in the present specimens but it makes an angle of considerably more than 90° with the anterior bar.

REMARKS. Collinson & Druce (in press) have discussed the relationships of this species with other lonchodinids.

Lonchodina paraclarki Hass

Plate 24, figs. 16a, b

- 1953 *Lonchodina paraclarki* Hass : 83, Pl. 16, figs. 15, 16.
 non 1958 *Lonchodina paraclarki* Hass ; Stanley : 468, Pl. 67, fig. 1.
 non 1958 *Lonchodina* cf. *paraclarki* Hass ; Rexroad : 22, Pl. 4, figs. 4, 5.
Lonchodina paraclarki Hass ; Collinson & Druce (in press).

MATERIAL. 3 specimens : figured, X 231.

RANGE. North Crop 3D 10-3D 14/15.

DESCRIPTION. The most distinctive features are the very short posterior bar tending to develop only 2 denticles, the massive incurved and recurved apical denticle, and the very strong inner-lateral deflection of its aboral margin, giving a sub-triangular basal cavity that extends along most of the aboral surface of the unit. Hass has discussed the relationship of the species to *Ligonodina clarki* (1953 : 83) and Collinson & Druce have discussed the differences between *Lonchodina paraclarki* in the original sense of Hass and specimens referred to that species by Stanley & Rexroad.

Lonchodina paraclaviger Rexroad

Plate 24, figs. 15a, b, 18a, b

- 1958 *Lonchodina paraclaviger* Rexroad : 22, Pl. 4, figs. 7-10.
Lonchodina paraclaviger Rexroad ; Collinson & Druce (in press).

MATERIAL. 780 specimens : figured X 232, X 233.

RANGE. North Crop 3D 13-3D 14/15.

DESCRIPTION. This species is characterized by its stout general construction. The posterior bar is about half the length of the anterior bar. The stout, basally confluent, elongated, pointed denticles, number eight on the anterior bar, and four on the posterior. Both bars are straight except for slight curvature in the anterior, where they make an angle of about 90°-100° with each other. The lateral deflection of the posterior bar is about 45° out of the vertical plane of the anterior bar, and a large flaring asymmetrical cavity is strongly developed on the inner side, as a sub-triangular, to rounded expansion, that is flat on the outer lateral face and is extended along both bars as a deep groove. Both bars are relatively deep, with convex lateral faces. The denticles of the anterior bar, although basally confluent, are discrete for most of their length, and approach the apical denticle in size ; they may be of uniform size or they may increase in size towards the anterior end of the unit ; they are slightly recurved posteriorly and also inwardly, and lie more or less parallel to the apical denticle, which is sometimes only slightly larger than those of the anterior bar. The apical denticle is very strongly convex on its inner lateral face, with sharp anterior and posterior edges, and rather less strongly convex on its outer lateral face ; it is more or less straight in lateral view but is inclined posteriorly at about 60° to the anterior bar and is also recurved inwardly. The denticles of the posterior bar tend

to be rather straight, but are discrete, sharply pointed, and tend to be directed inwardly, being either erect to the posterior bar or in a few cases sloping slightly forward ; in most specimens, however, they are either erect or posteriorly inclined. The posterior denticles tend to decrease in size posteriorly.

The basal cavity is strongly developed on the inner side of the unit, but it is wide, rather than deep ; it extends as a very narrow groove along the bars.

Lonchodina transitans Collinson & Druce

Plate 31, fig. 14

Lonchodina transitans Collinson & Druce (in press).

MATERIAL. 3 specimens : figured, X 234.

RANGE. North Crop 3D 4-3D 14/15.

DESCRIPTION. The present specimens are incomplete but they show the essential features of the species, including the angle of divergence of the anterior and posterior bars of about 130° and the more or less bilaterally asymmetrical open "lignodina" type cavity which is developed below the apical denticle. The apical denticle is recurved and relatively slender. The posterior bar is broken in the present specimens but bears at least 2 discrete, sharply pointed, posteriorly inclined denticles. The anterior bar is straight, and is slightly inflexed, as well as being depressed ; it bears at least 3 laterally compressed, recurved, slightly incurved denticles. Both bars are excavated by aboral grooves which extend into the shallow and rather flared cavity below the basal surface of the apical denticle. The apical denticle is biconvex in cross-section in its proximal part, and its strong lateral expansion on the outer face develops a suggestion of a median ridge on the lower part of that surface.

REMARKS. Collinson & Druce have pointed out that this species represents a transitional form between the genera *Lignodina* and *Lonchodina*.

Lonchodina sp. A

Plate 24, figs. 17a, b

MATERIAL. 6 specimens : figured, X 424.

RANGE. North Crop ZLA 32-ZLA 33.

DESCRIPTION. All the present specimens are broken, but they appear to represent a short unit, the bars being restricted. The apical denticle is large, laterally compressed and inclined toward the inner side. The bars appear to be curved on the outer side. The basal cavity is large and occurs beneath the apical denticle.

Genus *MAGNILATERELLA* Rexroad & Collinson 1963

1963 *Magnilaterella* Rexroad & Collinson : 11.

TYPE SPECIES. *Magnilaterella robusta* Rexroad & Collinson 1963.

Magnilaterella complectens (Clarke)

Plate 23, figs. 14a-17c

- 1900 *Prioniodus tulensis* Hinde (*partim*) : 343, Pl. 9, fig. 16.
 1928 *Prioniodus tulensis* Hinde ; Holmes (*partim*) : 22, Pl. 3, fig. 20.
 1960 *Ligonodina complectens* Clarke : 9, Pl. 1, figs. 14, 15.

MATERIAL. 14 specimens : figured, X 240, X 237, X 238, X 239.

RANGE. Scotland HOSIE 2A-HOSIE 2B.

DESCRIPTION. This species is clearly a member of the genus *Magnilaterella* Rexroad & Collinson, but is not typical of that genus. The generic features are seen in the present specimens in the short form, strong inner lateral callus and basal groove of the lateral bar, and the deflected and upflexed general form of the posterior bar, the largest denticles of which are situated at the proximal end and which are strongly developed and strongly recurved and incurved. In contrast to other described forms of the genus *Magnilaterella*, however, the largest denticles of the lateral bar are situated at the anterior, and not at the posterior end. This form, therefore, seems to approach *Ligonodina*, to which *Magnilaterella* is closely related. Rexroad & Collinson (1963 : 13) have discussed the relationships between the two genera, but the character of the present specimen alters the view of the distinctive nature of the denticulation of the posterior bar.

The lateral bar is short and in inner view is deep ; the most anterior denticle is enormously developed and strongly recurved in its lower portion, its distal half being more or less straight, although the distal posterior edge is so sharply pointed that it gives it almost a sigmoidal appearance. The two remaining denticles of the posterior bar are inconspicuous by comparison with the major denticle ; they are isolated, small, sub-circular, and more or less sharply pointed. The posterior bar is curved sharply backward and upward and the proximal denticle is very strongly developed. It approaches, but does not quite equal, the major denticle in size ; it is biconvex in cross-section, with bluntly developed anterior and posterior ridges in its upper half, but in the proximal half it is convex on the anterior face and has a concave posterior depression on its posterior edge. The inner lateral face is strongly convex and it bears at least one small isolated sub-circular denticle. The largest denticle of the posterior bar is recurved and deflected parallel to the major denticle.

The aboral surface of the unit is conspicuously grooved ; the outer aboral surface tends to be flat and rather extended below the major denticle, but the inner aboral surface is strongly developed as a callus, which runs up the inner face of the lateral bar. This slopes down to give a relatively narrow, horizontal, aboral surface, parallel to the base of the groove. In more complete specimens the lateral bar is seen to taper to a point at its distal end ; it may bear only 2 denticles including the most anterior denticle. In more complete specimens the posterior bar may bear up to 6 denticles in specimens which tend to decrease distally in size ; when viewed orally it makes an angle of about 30° with the lateral bar. In the specimen shown in Pl. 23, fig. 14 a small and relatively inconspicuous denticle is developed in front of the largest

denticle of the lateral bar, being about equal in height to the larger denticles of the posterior bar.

When viewed aborally the most striking feature of this species is the broad extension of the aboral surface, represented by the flange, and the restriction of the warped and flexed sinuous cavity to the outer lateral margin of the scar, which the flange forms.

Magnilaterella clarkei sp. nov.

Plate 23, figs. 11-13b

1900 *Polygnathus convexus* Hinde (*partim*) : 342, Pl. 9, fig. 7.

1928 *Lonchodus convexus* (Hinde) Holmes (*partim*) : 14, Pl. 6, fig. 14.

1960 "Gen. et sp. nov?" Clarke : 16, Pl. 11, figs. 10, 12, 13.

DERIVATION OF NAME. After Dr. W. J. Clarke.

DIAGNOSIS. *Magnilaterella* characterized by massive development of strongly depressed, continuously curved posterior bar, gently flexed inward in its median part, its denticles tending to be largest in its mid-third. Denticles of lateral bar large, sub-triangular, separated by smaller single denticles. Posterior bar of insignificant size in comparison with lateral bar, but strongly inflexed.

MATERIAL. 23 specimens : Holotype X 431, Paratypes X 241, X 432 (all figured).

RANGE. Scotland DUN 52-80, GILM 3-BIL 102.

DESCRIPTION. This is a rather typical species of the genus *Magnilaterella*, with a very elongated and very deep posterior bar, which becomes deeper in its posterior part. It has a very feebly convex inner-lateral face and is bowed slightly outwards along its length. It is continually recurved with a conspicuous concave aboral surface. The oral surface bears up to 4 main denticles, which tend to be largest in the median third and decrease in size in both directions. They are conspicuously triangular in lateral view and are sharply pointed. The denticles have very sharp

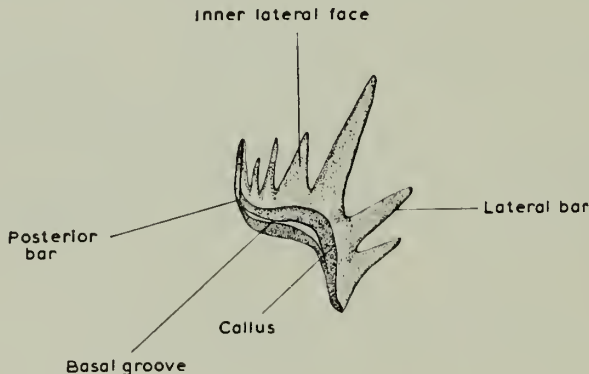


FIG. 29. *Magnilaterella* sp. showing morphological terms used in the text.

anterior and posterior edges and feebly convex to flat lateral faces. They are separated by a single similar denticle, widely spaced between them but only about one fifth to one sixth of the length of the larger denticles they separate. The posterior end of the lateral bar is marked by one such denticle which extends downwards to form the bluntly triangular distal end of the bar. At the anterior end of the lateral bar there are 2 to 3 smaller denticles of this general kind. The inner aboral surface of the posterior bar is marked by a variably developed flange, which although laterally persistent is irregular in the extent to which it invades the lateral face of the unit. It tends to do this to a rather small degree and its greatest aboral extension is under the posterior third of the bar.

The posterior bar is very small in comparison with the lateral bar and is strongly recurved, so that in oral view it makes an angle of about 30° with the lateral bar. It is also sharply convex and seems to bear rather small denticles although in the present specimens it is broken. The largest of these small denticles, occurs at its junction with the lateral bar. It tends to decrease in depth distally at its junction with the lateral bar, just anterior to the bluntly spatulate termination of the latter. In outer lateral view the outer lateral bar is flat and the outer lateral surface of the denticles are also markedly flat; only a few of them show any degree of convexity. There is no sign in outer lateral view of the scar-like presence of the inner callus. In aboral view a thin slit occurs along the length of the lateral blade and is also developed, though in much reduced width, below the posterior bar.

REMARKS. The specimens referred to this species show some variation in the development of the callus on the inner lateral face and also in the depth of the lateral bar, which tends in some specimens to be deeper in its medial third than its distal third.

Magnilaterella contraria sp. nov.

Plate 23, figs. 8a-c, 18a-c

1941 *Ligonodina* ? sp. Branson & Mehl : 171, Pl. 5, fig. 11.

1963 New Gen. et sp. Rexroad & Collinson : 21, Pl. 3, fig. 2.

DERIVATION OF NAME. With reference to the morphology.

DIAGNOSIS. *Magnilaterella* characterized by very delicate and slender construction. Short lateral bar bearing three isolated and recurved denticles, the largest being the middle : bar very shallow decreasing in height posteriorly, and making an obtuse angle with posterior bar.

MATERIAL. 3 specimens : Holotype X 553, Paratype X 517 (both figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample 3D 23.

RANGE. North Crop 3D 23.

DESCRIPTION. The lateral bar is short and more or less straight in a vertical plane but is strongly recurved, so that its basal surface is continuously concave in lateral view. It is of very slender construction and bears only 3 or 4 denticles, the two in the medial part being much larger than those at either end. The denticles are

recurved, but their axes are straight and sharply pointed ; they have sharp anterior and posterior edges and strongly convex lateral faces, their proximal portions tending to become flatter towards their apices ; they are about four to five times as long as the other denticles on the unit. The inner lateral face of the lateral bar is marked by a callus, which is not conspicuous and does not extend far up the lateral face : the bar decreases in width posteriorly and its posterior end is marked by a very small denticle, the posterior aboral margin being bluntly rounded ; the bar may be very slightly flexed outward in a vertical plane, but it is essentially straight.

The posterior bar is of unknown length ; it bears at least one small denticle near its junction with the lateral bar. It is excavated by a narrow groove which extends continuously below the lateral bar.

REMARKS. Rexroad & Collinson (1963 : 21), described forms closely similar to this species, but did not include them in the genus *Magnilaterella*. They did not state the reasons for this exclusion, but these presumably involve the relatively slight difference in the form of the basal cavity, which in the present specimens tends to be medial rather than lateral on the two bars, the restricted nature of the callus, and the fact that the posterior denticle of the lateral bar is not the largest of those developed.

Other specimens described above in the present paper show that none of these characteristics is wholly distinctive of the genus *Magnilaterella*. Some species which are, on all other morphological criteria, "good" species of the genus, do not have the posterior denticle more strongly developed than the rest of the series, and the form of the callus is a highly variable feature ; it, therefore, seems to us that there is no good reason for excluding this species from the genus.

Magnilaterella robusta Rexroad & Collinson

Plate 31, figs. 25, 26, 27

- 1941 *Lonchodina* sp. Branson & Mehl (*partim*) : 171, Pl. 5, fig. 10 only.
 1956 *Metalonchodina* ? sp. Elias : 124, Pl. 5, fig. 3.
 1957 Genus Indeterminate Rexroad (*partim*) : 42, Pl. 4, figs. 19-21 only.
 1958 Genus Indeterminate Rexroad : 26, Pl. 5, figs. 1, 2.
 1963 *Magnilaterella robusta* Rexroad & Collinson : 14, Pl. 2, figs. 4, 5, 9, text-figs. 3, 4.
 1964 *Magnilaterella robusta* Rexroad & Collinson ; Rexroad & Furnish : 673, Pl. 111, figs. 27-31.
 1965 *Magnilaterella robusta* Rexroad & Collinson ; Rexroad & Nicoll : 22, 23, Pl. 1, figs. 10, 11.

MATERIAL. 3 specimens : figured, X 528, X 529, X 548.

RANGE. Scotland Samples DUN 78-79.

DESCRIPTION. Well preserved specimens from our Scottish faunas are very closely similar to those illustrated and described by Rexroad and Collinson. The inner lateral process is short and stout, and is strongly recurved and very strongly arched. It bears up to 6 denticles, those near the apex being the largest. The posterior bar is small and relatively straight. It is strongly flexed and bears only 1 or 2 denticles, that nearest the anterior end being the largest.

Magnilaterella sp.

Plate 23, fig. 9

MATERIAL. 1 specimen : figured, X 244.

RANGE. Scotland GILM 2.

DESCRIPTION. A single specimen of doubtful affinities is referred to this genus. It is characterized by the distinctive callus developed on the inner face of the lateral bar and the slit-like excavation developed on both bars. The posterior bar is very short and may not be broken. The lateral bar bears two denticles which are discrete, inclined and sharply pointed ; the bar is broken and is of unknown length. The posterior bar bears a single denticle at its junction with the lateral bar ; the denticle is short but sharply pointed, being only about one sixth to one seventh the length of the posterior bar.

Magnilaterella spp.

Plate 23, fig. 10 ; Plate 31, figs. 5, 11

MATERIAL. 649 specimens : figured, X 242, X 322, X 323.

RANGE. Avon Gorge Z 35-C 24, North Crop CYD 6-3D 17.

DESCRIPTION. Fragmentary specimens of *Magnilaterella* are relatively common in the upper part of the D Zone and elsewhere. Few of them are sufficiently complete to enable specific identification, but some of them probably represent new species. We illustrate three extreme forms.

Plate 31, fig. 11 (X 322) shows a form with characteristically deep and strong posterior bar, the inner lateral face of which bears a well-developed callus and basal groove, which is thin but conspicuous and long. The apical denticle is very strongly developed, and has four to five times the basal width of other denticles of the posterior bar. The lateral bar is very strongly flexed, and the denticles decrease rapidly in size towards the distal end.

Plate 31, fig. 5 (X 323) shows a form characterized by much more slender construction. The apical denticle is elongated and gently curved posteriorly and inwards. It is sharply pointed and its general construction is slender. The callus is conspicuous, but shallow, and the lateral bar, which lies at about 90° in both a horizontal and vertical plane to that of the posterior bar, has its main flexure at its junction with the posterior bar rather than being continuously recurved.

Magnilaterella ? sp.

Plate 23, figs. 7a, b

MATERIAL. 1 specimen : figured, X 447.

RANGE. North Crop ZLA 37.

DESCRIPTION. This specimen consists of an antero-lateral and a posterior bar. The major denticle is smaller than the denticles on the posterior bar and lies in

between the planes of the two bars. The anterior bar is lateral and deflected, bearing 3 isolated denticles. The posterior bar bears 3 large, posteriorly inclined denticles.

Genus *MESTOGNATHUS* Bischoff 1957

1957 *Mestognathus* Bischoff : 36.

TYPE SPECIES. *Mestognathus beckmanni* Bischoff 1957.

DIAGNOSIS. A canoe-shaped form, with a well-developed platform, tapering to anterior and posterior. The platform ornamented by numerous transverse ridges. A high anterior blade developed on the outer side of the platform ; inner side of the platform, in lateral view, extends further to the anterior, than the outer side of the platform, because of the development of the anterior blade on the latter. A deep trough runs along mid-length of oral surface. Aborally a small narrow basal cavity present.

REMARKS. The genus *Mestognathus* Bischoff closely resembles *Cavusgnathus* Harris & Hollingsworth, but differs from the latter genus in that it has a small narrow basal cavity compared with the wide flaring basal cavity typical of *Cavusgnathus*. *Mestognathus* has not been recorded from North America and makes its first appearance in Europe in Cu II β/γ . In North America *Cavusgnathus* makes its first appearance at nearly the same horizon and so the two genera may be closely related.

Mestognathus beckmanni Bischoff

Plate 15, figs. 7a-d

1957 *Mestognathus beckmanni* Bischoff : 37, Pl. 2, figs. 4a, b, c, d, 5, 6, 8, 9.

1960 *Mestognathus beckmanni* Bischoff ; Kronberg, Pilger, Scherp & Ziegler : 14, Pl. 3, figs. 1a, b.

1962 *Mestognathus beckmanni* Bischoff ; Meischner : text-fig. 10.

1962 *Mestognathus beckmanni* Bischoff ; Bartenstein & Bischoff : Tab. 3.

MATERIAL. 36 specimens : figured, X 245.

RANGE. North Crop CYD 7, Avon Gorge C 15-D 26.

DESCRIPTION. The carina is restricted to the posterior part of the platform in this species, but may in some cases be extended anteriorly to meet the inner lateral face at a narrow angle. The anterior blade is high and has from 6 to 12 denticles which occupy the anterior margin of the outer side of the platform. The medial trough is deep and very wide, and runs for at least half the length of the platform, being deepest anteriorly. The unit is about four times as long as it is wide, being widest at about mid-length of the platform. In outer lateral view the highest part of the anterior blade is about twice the depth of the posterior platform at mid-point. The anterior blade is characterized in lateral view by the development of from 6 to 12 denticles which are basally fused, only their tips being discrete. They tend to be of variable size and to have bluntly rounded apices with gently convex lateral faces. The largest denticles are the posterior one or two on the blade, especially the most

posterior. This tends to be sub-triangular in form, and is inclined posteriorly, with strongly convex lateral faces and blunt anterior and posterior edges. Its inner lateral face is flatter than its outer. The other denticles stand more or less erect to the bar but their inclination is rather variable. The anterior blade is inclined gently inwards; there is a tendency for the denticles, to show some reduction in height anteriorly and the anterior blade projects beyond the platform at the anterior end.

In oral view a deep trough is developed parallel to the anterior blade, being widest and deepest anteriorly. It shallows towards the position of maximum width of the posterior platform and becomes obsolescent in the posterior half. It is broadly U-shaped. The outer margins of the carina are decorated with feeble to moderate transverse ornament, which tends to be aligned acutely to the length of the unit, forming an arrow-type structure pointing forward, rather than being developed at right angles. There are about 12 of these ridges on the outer side of the platform and about 17 on the inner. They become rapidly obsolescent towards the middle of the platform and are more feebly developed on the inner than on the outer side. There is a variable posterior carina developed in the posterior part of the unit, consisting of a low ridge of only barely distinguishable nodose denticles, but it may be extended anteriorly to meet the antero-lateral inner edge of the platform as a low inconspicuous ridge, dividing the platform into two unequal parts. It runs to the left of the medial trough. The outline of the platform in oral view is such that the anterior two-thirds of the inner lateral margin is straight and the posterior third inclined towards its pointed posterior termination. The outer lateral face is straight in its anterior half and gently concave in its posterior half, the whole appearance of the unit being pinched towards the posterior fifth. The anterior inner lateral edge terminates in an undenticulate projection. The edges of the platform are feebly up-turned. In inner lateral view the antero-inner face of the platform is flat, with sharp oral and aboral lateral edges. The lateral face decreases in width towards the mid-point, beyond which the platform has a thin lateral face which merges with the base. The outer lateral face is characterized by having a flat surface, parallel to the denticles, with a longitudinal ridge developed about the base of them, and then a sloping lateral face which slopes towards the basal cavity below the ridge. In outer lateral view the posterior half has a lateral face, which slopes steadily towards the basal cavity.

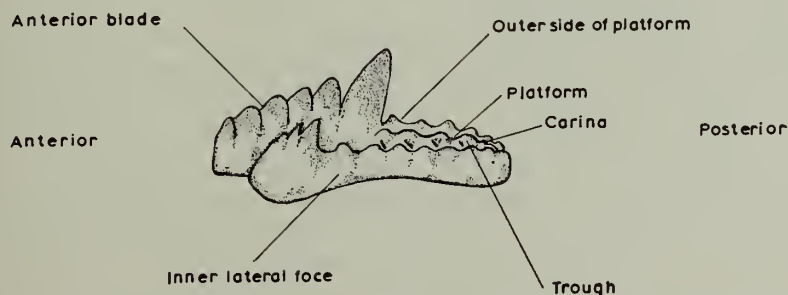


FIG. 30. *Mestognathus* sp. showing morphological terms used in the text.

The basal surface is characterized by a restricted median cavity, which is shallow and occupies the anterior half of the platform. It extends anteriorly and posteriorly as a very narrow shallow slit along the unit.

Mestognathus bipluti Higgins

Plate 25, figs. 1a-3c, 8a, b

1961 *Mestognathus bipluti* Higgins : 216, Pl. 10, figs. 1, 2 ; text-fig. 4.

DIAGNOSIS. This species is characterized by a short, deep blade which diverges at the anterior end of the unit from the antero-inner lateral edge of the platform. Slender and pointed platform has a more or less prominent median carina.

MATERIAL. 3 specimens : figured, X 249, X 248, X 246, X 247.

RANGE. North Crop CYD 6-CYD 7.

DESCRIPTION. This species of conodont has an outline that is reminiscent to some extent of a folsom-point. The inner edge of the platform is straight in the anterior two thirds and then turns rapidly inwards towards the pointed posterior end. The posterior third is also straight and the bend is sharply angular. The outer lateral margin of the platform is straight in its anterior third and up to the end of the anterior blade, but posteriorly it is turned sharply inwards towards the pointed posterior end. The posterior outer lateral face is more or less straight. There is a strongly developed posterior carina, which consists of a series of confluent nodes, and extends about half the length of the platform. It is continued less obviously anteriorly to meet the antero-inner lateral point as a low inconspicuous ridge. There is a narrow deep trough adjacent to the blade and this becomes shallower and obsolescent posteriorly, extending on the outer side of the median carina. The inner lateral portion of the platform adjacent to the carina tends to be flat or feebly concave. The margins of the platform are ornamented by relatively strongly developed transverse ridges, which tend to become less conspicuous towards the posterior end. They extend about half the distance from the lateral margins to the carina. The lateral margins themselves are gently up-flexed. The downward and outward curvature of the antero-aboral portion of the blade is a conspicuous feature in oral view, as is the divergence of the anterior blade and the antero-inner edge of the platform to give a branched structure.

In aboral view this latter feature is the most conspicuous characteristic of the species. The total length of the branches are a third to a quarter of the length of the platform. The medial cavity is very small and inconspicuous and is only slightly flared. It extends anteriorly and posteriorly as a keeled narrow slit along the median line of the unit. The main cavity is situated near the junction of the blade.

In inner lateral view the oral surface of the unit is bluntly serrated and the posterior end is bluntly spatulate. In outer lateral view the aboral margin is straight in the posterior half, but gently concave in the anterior half. In outer lateral view the anterior blade is a very distinctive feature. The posterior denticle is the largest and the blade decreases regularly in depth towards the bluntly spatulate anterior end.

The denticles form a fused series of bluntly pointed confluent denticles, about 5 or 6 in number, grading in the antero-aboral region into minute and inconspicuous confluent denticles. The antero-aboral portion is flexed sharply outwards; the posterior denticle is inclined slightly posteriorly. The whole posterior outer lateral face of the platform slopes gently inwards to meet the basal slit, giving a boat-like appearance to the unit in lateral view. It is convex to flat in its upper part and may become concave in its postero-aboral portion. In inner lateral view the same feature is seen. The platform is relatively straight in its posterior third, but is regularly concave in its anterior third or half. The inner lateral margin is generally developed at a lower level than the outer lateral margin, and is finely denticulated, the inner anterior edge of the platform bearing rather conspicuous low denticles. The antero-aboral inner edge is strongly convex and is deflected inwards. It is much less deep than the corresponding outer aboral anterior edge.

Mestognathus neddensis sp. nov.

Plate 15, figs. 4a-6c

DERIVATION OF NAME. From the River Nedd, Breconshire.

DIAGNOSIS. Mestognathid with short deep anterior blade, bearing 6 denticles, those at anterior end being only slightly shorter than those at posterior; their apices are discrete. Anterior blade and inner anterior edge of platform bifurcate at the anterior end of the unit. Posterior platform straight on outer lateral side and gently convex on inner lateral side, posterior inner lateral portion being strongly pinched inwards towards pointed posterior end. Strong posterior carina, consisting of low rounded nodes along posterior half of platform, becoming obsolescent towards anterior inner lateral edge of platform.

MATERIAL. 5 specimens: Holotype X 250, Paratypes X 251, X 252 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample CYD 6.

RANGE. North Crop CYD 6-CYD 7.

DESCRIPTION. In oral view the unit is elongated and slender. The anterior blade is free for only a very small portion of its length, but the anterior end of the platform is marked by a V-shaped indentation, formed by the junction of the anterior blade and the inner anterior margin of the platform. The blade is conspicuously denticulated in oral view and the outer lateral margin of the platform is more or less straight. It is ornamented by a series of transverse denticles which are more strongly developed in the anterior portion than the posterior. The inner lateral platform is gently sinuous, being straight to gently concave in the anterior third and strongly convex in the posterior two thirds. The posterior carina extends beyond the posterior limit of the platform, so the whole appearance of the platform is rather pinched posteriorly. The inner lateral margin of the platform is ornamented by feeble, nodular to transverse ridges which become obsolescent towards the anterior part. The posterior half of the platform is marked by a conspicuous carina, consisting of 7 or 8 low rounded fused nodes, and is extended as a rather inconspicuous ridge towards the

anterior inner lateral edge of the unit. There is a narrow V-shaped trough developed adjacent to the blade, running towards the posterior end of the unit on the outer margin of the carina, and becoming shallower and narrower posteriorly. In outer lateral view the blade is conspicuously deeper than the platform. It is of regular depth throughout its length and in some specimens shows a tendency to increase anteriorly in depth. It is very bluntly rounded antero-aborally, and is strongly down-flexed in relation to the blade. Although the junction between the two is curved, the anterior aboral edge of the blade makes an angle of about 45° with the aboral edge of the posterior platform. The oral surface of the blade bears 6 or 7 fused denticles, the apical tips of which are discrete and bluntly rounded.

In outer lateral view the posterior platform has a bluntly serrated surface and its outer lateral face slopes down sharply towards the median aboral keel. The posterior end is more or less flat, and the denticles of the posterior median carina tend to be higher in outer lateral view than those on the edge of the platform. The posterior third of the platform is straight, but the anterior part is gently concave. The denticles of the anterior blade are more or less uniform in height, although the most posterior tends in some specimens to be rather larger than the rest. They are more or less erect, though the most posterior denticle may be slightly inclined posteriorly.

In inner lateral view the aboral surface of the whole unit appears to be gently convex, except for the rather straight posterior termination. The oral edge is more or less conspicuously serrated by low nodose confluent nodes, and the anterior inner edge is frequently developed into one or two rather conspicuous denticles, its antero-aboral margin being bluntly pointed and making a very prominent bifid junction with the anterior blade. The extension of the posterior carina is a prominent feature in this inner lateral view. The inner oral margin of the platform is strongly convex, but it flattens off along the mid-height of the unit, and the lower part is flat to strongly concave, sloping rapidly towards the elongated aboral keel.

In aboral view there is a prominent, but very small, median pit with inconspicuous edges, which is developed near the junction of the blade of the platform. It is biconvex in outline and is elongated antero-posteriorly. A shallow rather flat aboral surface extends posteriorly from it along the unit with an inconspicuous median slit developed towards the posterior end. Anteriorly a thin slit runs towards the junction of the inner anterior edge with the anterior blade.

The posterior end of the platform is marked by a more or less vertical face, with rounded posterior aboral margin. The platform deepens towards the anterior inner edge when seen in inner lateral view, and this is a conspicuous feature of the unit.

Genus *METALONCHODINA* Branson & Mehl 1941

TYPE SPECIES. *Prioniodus bidentatus* Gunnell 1931.

Metalonchodina bidentata (Gunnell)

Plate 24, figs. 8a-11b

1900 *Polygnathus convexus* Hinde (*partim*) : 342, Pl. 9, fig. 8.

- 1928 *Lonchodus convexus* (Hinde) Holmes (*partim*) : 14, Pl. 6, fig. 13.
 1931 *Prioniodus bidentatus* Gunnell 247, Pl. 29, fig. 6.
 1933 *Prioniodus dactyloodus* Gunnell 265, Pl. 31, fig. 1.
 1941 *Metalonchodina bidentata* (Gunnell) Branson & Mehl : 106, Pl. 19, fig. 34.
 1941 *Metalognathus bidentata* (Gunnell) Ellison : 116, Pl. 20, figs. 35, 36.
 1952 *Metalognathus bidentata* (Gunnell) Rhodes : 898, Pl. 128 'm' .
 1957 *Metalonchodina bidentata* (Gunnell) Bischoff : 37, Pl. 5, figs. 13, 15, 46.
 1960 *Metalonchodina confecta* Clarke : 17, Pl. 2, fig. 14.
 1961 *Metalonchodina bidentata* (Branson & Mehl) Higgins : Pl. 12, fig. 9.
 1962 *Metalonchodina bidentata* (Gunnell) Higgins : Pl. 1, fig. 3.
 1964 *Lonchodina ? nipponica* Igo & Koike : 186, Pl. 27, fig. 20.
 1964 *Metalonchodina* sp. Rexroad & Furnish : 673, Pl. 111, fig. 7.
 1965 *Metalonchodina fragilis* Murray & Chronic : 605, Pl. 73, figs. 19, 20.
Metalonchodina bidentata (Gunnell) Collinson & Druce (in press).

MATERIAL. 6 specimens : figured, X 253, X 254, X 255, X 256.

RANGE. North Crop 3D 10-3D 14/15.

DESCRIPTION. The present specimens agree closely with Branson & Mehl's (1941 : 106) definition of the species. The anterior limb is shorter than the posterior bar and bears a massive denticle or pair of denticles upon it. In aboral view the most conspicuous feature is the very strong lateral flexing below the apex of the two bars. The small and fairly shallow pit is situated in the middle of the strongly laterally expanded aboral surfaces at this point ; the aboral surfaces of each limb being relatively flat or obtusely V-shaped. They are excavated by very narrow shallow slit-like cavities along their lengths. The chief expansion of the base below the apical denticle is concentrated on the inner lateral side and is a very prominent feature of the unit. In inner lateral view the most conspicuous feature of the unit is the enormous size of the denticle developed on the anterior bar. This is about two to three times as wide as any of the other denticles, has straight anterior and posterior edges and is bluntly pointed. It has gently convex inner and outer lateral faces. The anterior edge of the unit is developed into a triangular pointed anterior end. Its aboral margin is straight, and although its junction with the posterior bar is curved, it makes an angle of 80°-90° with the aboral surface of the latter. The posterior bar bears two or three smaller denticles, sub-circular in cross-section, with inconspicuous anterior and posterior edges, which are inclined anteriorly.

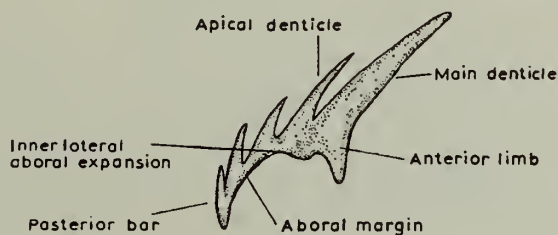


FIG. 31. *Metalonchodina* sp. showing morphological terms used in the text.

The apical denticle is smaller than the large denticle on the anterior bar but of similar general form. Its most conspicuous feature is the very strong, internal lateral extension of the aboral portion, to form the inner lateral flange. On the aboral margins both the anterior and the posterior bars are more or less straight. Their most striking feature in inner lateral view is the development of a longitudinal ridge parallel to their bases, which rises higher on the faces towards the apex, and represents the bevelled margin of the flattened aboral surface.

In lateral view this latter feature is less conspicuous and the whole unit is flat to feebly convex in general form.

REMARKS. This species shows appreciable variation. The specimens illustrated in Pl. 24, figs. 8, 10 and 11 are closely similar. That of Pl. 24, fig. 9, resembles them in overall form but has an additional denticle developed anterior to the main denticle of the anterior bar, and the apical and posterior denticles also tend to be more sub-circular than those of typical members of the species. Similarly, other specimens have two smaller denticles developed anterior to the main denticle of the anterior bar and also have more sub-circular denticles. It may be that these specimens should be regarded as distinct species but they are provisionally included in *Metalonchodina bidentata*.

Genus *NEOPRIONIODUS* Rhodes & Muller 1956

1956 *Neoprioniodus* Rhodes & Müller : 698.

TYPE SPECIES. *Prioniodus conjunctus* Gunnell 1931.

Neoprioniodus antespathatus Collinson & Druce

Plate 21, figs. 10a-11b

Neoprioniodus antespathatus Collinson & Druce (in press).

MATERIAL. 2 specimens : figured, X 257, X 258.

RANGE. North Crop 3D 8-3D 16.

DESCRIPTION. This is a neoprioniodid with a slender anteriorly directed anterior denticle, with sharp anterior edge, blunt posterior edge, and biconvex outline. The posterior bar is slender, decreasing in depth posteriorly, and it has a conspicuously concave junction with the aboral process. Its oral surface bears a series of about 9 denticles, the largest of which are in the anterior half, and which show a broad tendency to decrease in size posteriorly, though this tendency is not conspicuous or regular. The denticles are basally confluent, but are discrete for most of their length. They are of slender general form, with sharp anterior and posterior edges

and gently convex lateral faces. They stand more or less erect or gently posteriorly inclined in relation to the underlying aboral surface of the bar. The posterior bar is gently down-curved, although its distal portion is more or less straight. The aboral projection of the anterior denticle is the most massive feature of the unit. It is about twice as wide in lateral view as the basal part of the anterior denticle itself. Its anterior margin is straight to very gently concave and its anterior aboral termination is bluntly pointed. Its posterior aboral margin is very strongly convex and it decreases in width towards its distal end. The whole effect is of a massive structure. Its lateral faces are more or less flat but the whole unit is feebly curved inwardly.

In outer lateral view the whole unit is convex, reflecting the inward recurvature. In aboral view there is a very inconspicuous cavity developed below the apical denticle; the aboral surfaces of the posterior bar and the aboral process are flat in general form, the inner lateral aboral edge being slightly higher than the lower, and the whole surface is excavated by a minutely narrow and shallow longitudinal groove.

The most conspicuous features of this unit are the slender form of the anterior denticle and the posterior bar, in contrast to the massive form of the aboral process, the whole anterior lateral aboral face of which is more or less concave.

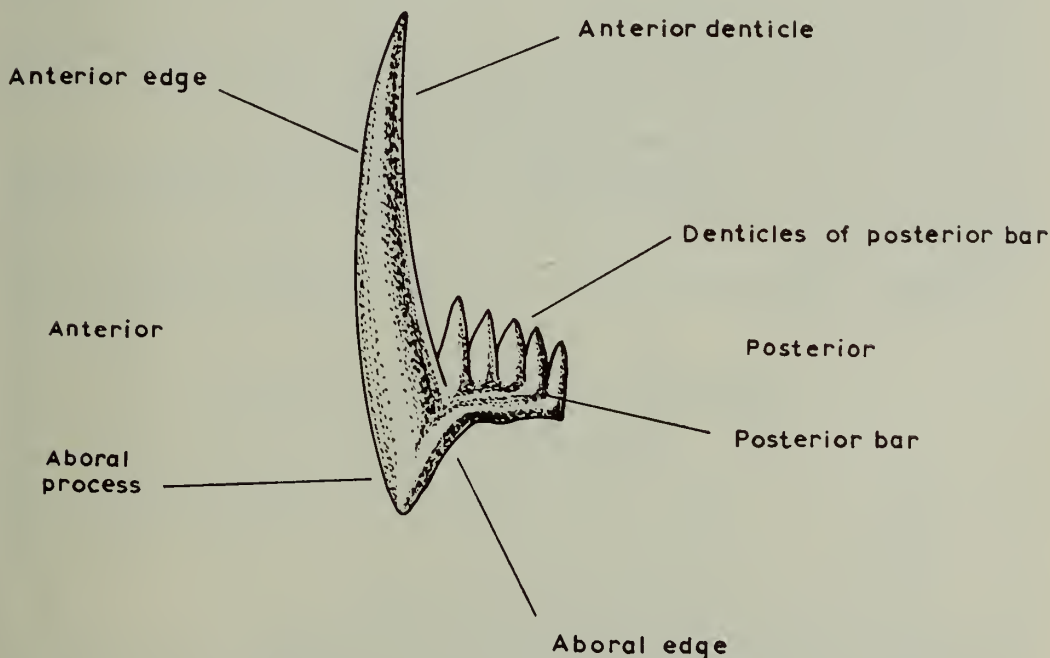


FIG. 32. *Neoprioniodus* sp. showing morphological terms used in the text.

Neoprioniodus barbatus (Branson & Mehl)

Plate 21, figs. 4-7

- 1934 *Prioniodus barbatus* Branson & Mehl : 288, Pl. 23, figs. 19, 20.
 1934 *Prioniodus corniger* E. R. Branson : 329, Pl. 28, fig. 2.
 1938 *Prioniodus barbatus* Branson & Mehl ; Branson & Mehl : 144, Pl. 33, fig. 21, pl. 34, figs. 28, 32.
 1938 *Prioniodus corniger* (?) E. R. Branson ; Branson & Mehl : 143, Pl. 34, fig. 19.
 1944 *Prioniodus barbatus* Branson & Mehl ; E. B. Branson : 221, Pl. 39, figs. 28, 32.
 1944 *Prioniodus corniger* (?) E. R. Branson ; E. B. Branson : 221, Pl. 39, fig. 19.
 1949 *Prioniodus barbatus* Branson & Mehl ; Thomas : 411, Pl. 4, fig. 26.
 1949 *Prioniodus corniger* E. R. Branson ; Thomas : 411, Pl. 4, fig. 27.
 1956 *Prioniodina barbata* (Branson & Mehl) Bischoff & Ziegler : 160, Pl. 13, figs. 19, 20.

MATERIAL. 674 specimens : figured, X 259, X 260, X 261, X 262.

RANGE. North Crop KL 13-ZL 9, Avon Gorge K 21-C 16.

DESCRIPTION. The anterior denticle is very tall, slender, laterally compressed, and ovate in cross-section. It is continuously and gently recurved toward the posterior, terminating in a fine point. The posterior bar is fairly deep, being deepest at the anterior and shallowing regularly towards the posterior. It bears 9 to 12 tall needle-like denticles, sub-circular in cross-section, which are fused at their bases but free at their tips. In the posterior part there is some twisting of the bar and it is down-curved slightly.

The basal cavity is situated on the aboro-posterior side of the anterior denticle, which is produced below the posterior bar to form an aboral process. The complete aboro-posterior surface is excavated, though there is comparatively little flaring of the lips, and the cavity may run for a short distance beneath the posterior bar. In most specimens the aboro-posterior outline of the aboral process is gently convex, but in some specimens a flange tends to develop, making it sigmoidal in outline (e.g. Pl. 21, fig. 6).

REMARKS. This appears to be a very common Avonian species, especially in the middle of the Z Zone.

Neoprioniodus confluens (Branson & Mehl)

Plate 21, figs. 2a, b, 8a, b

- 1934 *Prioniodus confluens* Branson & Mehl (*partim*) : 206, Pl. 15, fig. 6, (*non* Pl. 15, fig. 7=*N. alatus*).
 1934 *Euprioniodina prona* Huddle (*partim*) : 52, Pl. 6, fig. 19, (*non* Pl. 11, fig. 8=*Euprioniodina alternata*).
 1939 *Prioniodus alatus* Hinde ; Cooper : 404, Pl. 46, figs. 6, 8.
 1949 *Prioniodus aphanes* (Cooper) Thomas : 411, Pl. 4, figs. 20, 34.
 1949 *Prioniodus obtusus* Branson & Mehl ; Thomas 408, Pl. 1, figs. 1, 7.
 1955 *Prioniodus prona* (Huddle) Sannemann (*partim*) : 152, Pl. 3, fig. 1 only.
 1957 *Prioniodina prona* (Huddle) Ziegler in Flügel & Ziegler : 49, Pl. 4, fig. 6.
 1961 *Neoprioniodus armata* (Hinde) Scott & Collinson (*partim*) : 127, Pl. 2, fig. 24, (*non* Pl. 2, fig. 22=*N. armata*).

LECTOTYPE (here selected). The original of Branson & Mehl : 1934, 206 ; Pl. 15, fig. 6 only, University of Missouri C 365-5.

MATERIAL. 672 specimens : figured, X 264, X 263.

RANGE. North Crop KL 1-ZLA 33, Avon Gorge K 3-C 7.

DESCRIPTION. The anterior denticle is tall and narrows gradually to a pointed extremity. It is produced aborally into an aboral process. The posterior bar, which is straight or gently down-curved, is also deflected through 45° and slightly twisted. It bears a series of erect laterally compressed denticles, which are either fused or are in close proximity. The bar is very long and may possess up to 40 denticles which alternate in size. The basal cavity is situated at the junction of the posterior bar and the aboral process. It has a flared lip to produce a characteristic flange.

REMARKS. This is one of the most easily recognizable neoprioniodids owing to the large aboral process of mature specimens and the cavity flange. Frequently only the anterior denticle and cavity flange are preserved. Branson & Mehl (1934 : 206) described two co-types of the species *Prioniodus confluens* (Catalogue numbers C 365-5, University of Missouri). These appear to represent different species and we hereby designate the specimen illustrated in Pl. 15, fig. 6, as the lectotype of *Neoprioniodus confluens* (Branson & Mehl). This is given the same Catalogue Number as the other co-type (C 364-5).

One specimen (Pl. 21, figs. 1a-c) shows extreme regularity of dentition and it is only tentatively compared with this species.

Neoprioniodus conjunctus (Gunnell)

Plate 21, figs. 16a-17b, 20a, b

- 1926 *Prioniodus* sp. B (Roundy) (*partim*) : 11, Pl. 4, fig. 12 only.
 1931 *Prioniodus conjunctus* Gunnell : 247, Pl. 29, fig. 7.
 1933 *Prioniodus cacti* Gunnell : 263, 265, 267, Pl. 31, figs. 4 to 5.
 1933 *Prioniodus* sp. Gunnell : 264, 267, Pl. 32, fig. 32.
 1941 *Prioniodus conjunctus* Gunnell ; Ellison : 108-111, 113, 114, Pl. 20, figs. 1-3, 16.
 1941 *Prioniodus bulbosus* Ellison : 108-111, Pl. 20, figs. 4-7.
 1944 *Prioniodus conjunctus* Gunnell ; E. R. Branson : 327.
 1949 *Prioniodus cacti* Gunnell ; Youngquist & Downs : 169, Pl. 30, figs. 16, 17.
 1953 *Prioniodus inclinatus* Hass : 87, Pl. 16, figs. 10-14.
 1956 *Neoprioniodus conjunctus* (Gunnell) Rhodes & Müller : 3.
 1957 *Prioniodina bulbosa* (Ellison) Bischoff : 46, Pl. 5, fig. 37.
 1960 *Neoprioniodus brevis* Clarke : 13, 14, Pl. 2, fig. 7.
 1961 *Neoprioniodus inclinatus* (Hass) Higgins : 220, Pl. 11, fig. 3.
 1962 *Neoprioniodus conjunctus* (Gunnell) ; Higgins : 10, Pl. 1, fig. 2.

MATERIAL. 7 specimens : figured, X 265, X 267, X 266.

RANGE. North Crop 3D 14/15, Avon Gorge Z 35-C 7.

DESCRIPTION. The present specimens agree perfectly with Gunnell's holotype and with Ellison's (1961) descriptions and illustrations. The massive, blade-like anterior denticle, with the deep posterior bar consisting of confluent, strong denticles, up to about 4 in number, are very conspicuous features of the species. However, the

posterior bar is strongly laterally compressed and is relatively thin, being more or less triangular in section, with the aboral edge being the widest. The lateral faces are flat to feebly concave. The denticles of the posterior bar are strongly laterally compressed and are confluent for most of their length. They are bluntly pointed and have more or less sharp anterior and posterior edges, their lateral faces being feebly biconvex. The denticles proper are about twice the length of the posterior bar. The anterior denticle is very strongly developed; it is massive in general form, being about five times the length and two or three times the width of the largest denticles of the posterior bar. It is slightly recurved posteriorly, but its distal portion is more or less straight. It has very sharp anterior and posterior edges and is so strongly compressed in lateral view that it has a sword-like appearance. It is bluntly pointed. Its inner aboral lateral face is very strongly extended inwards, and this is a most conspicuous feature of the unit in lateral view. Its outer lateral face is feebly convex to flat in the lower part and is gently convex in the upper portion. The whole unit is very slightly curved in a horizontal plane, the inner side being feebly concave. In aboral view the most striking feature is the wide flaring of the inner lateral aboral edge around the junction of the anterior denticle and the posterior bar. The outer lateral face is less conspicuously flared. The whole aboral surface below this lateral flexure is excavated, culminating in a deep median pit which is restricted in its area, but extends anteriorly and posteriorly as rather conspicuous longitudinal grooves along the anterior portion of the anterior denticle and along the posterior bar. The posterior aboral edge of the anterior denticle makes an angle of about 120° with the straight edge of the posterior bar. The antero-aboral corner is very slightly convex and the junction with the edge is more or less pointed.

Neoprioniodus montanaensis (Scott)

Plate 22, figs. 5a-8b

- 1942 *Lochreia montanaensis* Scott (*partim*): 289, Pl. 29, fig. 9 only, Pl. 40, fig. 12.
 1941 *Prioniodus barbatus* Branson & Mehl; Ellison & Graves (*partim*): 3-4, Pl. 1, fig. 25 only.
 1953 *Prioniodus singularis* Hass: 88, Pl. 16, fig. 4.
 1956 *Prioniodus* cf. *singularis* Hass; Elias: 112, Pl. 2, fig. 45.
 1956 *Prioniodus roundyi* var. *dividen* Elias: 110, Pl. 2, figs. 39-41.
 1957 *Prioniodina alatoidea* (Cooper) Bischoff: 45, Pl. 5, figs. 33, 34, 36.
 1957 *Prioniodus* sp. A Ziegler in Flügel & Ziegler: 50, Pl. 4, fig. 3.
 1958 *Neoprioniodus singularis* (Hass) Stanley: 471, Pl. 66, figs. 2, 3.
 1958 *Neoprioniodus* sp. A Stanley: 472, Pl. 66, figs. 4, 5.
 1961 *Neoprioniodus singularis* (Hass) Higgins: Pl. 11, fig. 5.
 1962 *Neoprioniodus singularis* (Hass) Higgins: Pl. 1, fig. 8.
 1963 *Neoprioniodus singularis* (Hass) Bouckaert & Higgins: 17, fig. 3.
Neoprioniodus singularis (Hass) Collinson & Druce (in press).

MATERIAL. 232 specimens: figured, X 268, X 270, X 269, X 271.

RANGE. North Crop CYD 6-3D 19.

DESCRIPTION. The most distinctive feature of this species is the long, slender,

blade-like anterior denticle, which is enormously elongated in comparison with its rather slight aboral process. The latter is only about one-sixth to one-seventh the total length of the denticle. The posterior bar is also conspicuous, being short and sharply down-curved. The denticles of the posterior bar show a sharp decrease in length towards the posterior end of the bar. Those adjacent to the anterior denticle tend to be greatly elongated in comparison with those that follow. All are slender, with more or less sharp anterior and posterior edges, and gently convex lateral faces. They are discrete for about half their length and are regularly pointed. The whole unit is more or less strongly curved inwards in a horizontal plane.

The anterior denticle is greatly elongated and is very slender in its general form, being bluntly to sharply pointed at its apical tip. It extends as an aboral process only for a short distance, about one-sixth to one-seventh of its total length, below the level of the posterior bar. The anterior and posterior edges are generally straight, though in a few specimens they may be feebly recurved, and in other specimens there is a very slight anterior flexure of the aboral process. The anterior denticle has sharp anterior and posterior edges and gently convex lateral faces. It stands erect to the anterior portion of the posterior bar. The aboral process is more or less sharply pointed and triangular in form, without any conspicuous lateral flaring developed on the inner aboral margin. The anterior denticle is slightly curved inward in its distal third. The denticles of the posterior bar range from 10 to 21 in number and show a marked decrease in size posteriorly. The 2 adjacent to the anterior denticle are virtually confluent with it, only their apices being discrete. The remaining denticles of the posterior bar tend to be smaller and to be inclined more sharply posteriorly. They are discrete for about half their total length in complete specimens. The posterior bar shows a marked decrease in depth from the anterior to the posterior end. The posterior terminus is bluntly rounded. It has more or less flat to gently convex lateral faces, and a sharply bevelled aboral margin on both the inner and outer lateral faces. The whole unit is recurved inwardly in a horizontal plane. There is a relatively inconspicuous cavity below the anterior denticle, which extends as a shallow slit along the posterior bar and the antero-aboral process.

REMARKS. Hass (1953 : 88) erected the species *Prioniodus singularis* to include the present specimens. However, because the species was illustrated and described by Scott, even as part of a natural assemblage, it seems to us that his name must have priority. We, therefore, regard *Prioniodus singularis* Hass (1953 : 88, Pl. 16, fig. 4) as a junior synonym of Scott's species.

Neoprioniodus peracutus (Hinde)

Plate 21, figs. 12a-15b

- 1900 *Prioniodus peracutus* Hinde (*partim*) : 343, Pl. 10, fig. 22 only.
1926 *Prioniodus peracutus* Hinde ; Roundy : 10, Pl. 4, fig. 6.
1928 *Prioniodus peracutus* Hinde ; Holmes : 21, Pl. 3, fig. 38.
1953 *Prioniodus ligo* Hass : 87, Pl. 16, figs. 1-3.
1957 *Neoprioniodus erectus* Rexroad : 34, Pl. 2, figs. 23, 25.

- 1957 *Prioniodina cassilaris* (Branson & Mehl) Bischoff : 46, Pl. 5, figs. 27-31.
 1960 *Neoprioniodus peracutus* (Hinde) Clarke : 14, Pl. 2, fig. 6.
 1964 *Neoprioniodus peracutus* (Hinde) Rexroad & Furnish : 674, Pl. III, fig. 25.

MATERIAL. 32 specimens : figured, X 272, X 273, X 274, X 275.

RANGE. North Crop 3D 4-3D 22.

DESCRIPTION. A slender neoprioniodid in which the anterior denticle is continued more or less vertically downward to form the aboral process. There is a slender and highly recurved posterior bar, the straight postero-aboral portion of which makes an angle of about 130° with the posterior edge of the anterior denticle. The posterior bar decreases in depth posteriorly, its posterior termination being bluntly pointed, its antero-aboral surfaces gently concave, and its postero-aboral surface gently convex in lateral view. In outer lateral view its face is flat, and the whole unit is curved slightly inward so that its inner margin is concave. The oral surface of the posterior bar bears about 19 denticles which tend to decrease in height posteriorly. They are basally confluent, but apically discrete, being bluntly pointed, with sharp anterior and posterior edges and convex lateral faces. The denticles tend to be most conspicuously discrete in the anterior third of the bar, those towards the posterior portion being coalesced for the greater part of their length, but being discrete in their apical region.

The anterior denticle is slightly offset inwardly from the main line of the posterior denticles. It has sharp anterior and posterior edges, a feebly convex outer lateral face, and a rather flat antero-inner surface which extends downwards into the flat aboral process. The anterior edge of the aboral process is more or less straight, and the posterior aboral edge is regularly but feebly convex, giving the whole aboral extension a slender plough-like appearance. In inner lateral view, the inward deflection and curvature of the anterior denticle are well seen ; the antero-aboral face of the anterior denticle tends to be slightly concave, but otherwise the inner lateral face is more or less flat to feebly convex in its upper portion. Its anterior aboral edge bears two minor irregularities, but these are not sufficiently distinct to be recognized as denticles. The interior aboral edge of the anterior denticle is expanded, but not strongly so, and there is a very shallow longitudinal pit developed which extends along the flattened basal surface of the posterior bar ; the anterior part of the denticle has longitudinal slit-like grooves.

Neoprioniodus scitulus (Branson & Mehl)

Plate, 22, figs. 9a-10b, 12a, b

- 1939 *Prioniodus peracutus* Cooper : 406, Pl. 46, fig. 7.
 1940 *Prioniodus scitulus* Branson & Mehl : 173, Pl. 5, figs. 5, 6.
 1947 *Prioniodus scitulus* Branson & Mehl ; Cooper : 92, Pl. 20, figs. 1-3.
 1949 *Prioniodus* spp. Youngquist & Miller : 62, Pl. 101, figs. 9, 10, 14.
 1956 *Prioniodus scitulus* Branson & Mehl ; Elias : 109, Pl. 2, figs. 9, 10.
 1957 *Neoprioniodus scitulus* (Branson & Mehl) Rexroad : 35, Pl. 2, figs. 22, 26.
 1957 *Neoprioniodus striatus* (Branson & Mehl) Rexroad : 35, Pl. 2, figs. 11, 12.
 1957 *Prioniodina cassilaris* Branson & Mehl ; Bischoff : 46, 47, Pl. 5, figs. 27-31.

- 1958 *Neoprioniodus scitulus* (Branson & Mehl) Rexroad : 23, 24, Pl. 5, figs. 10-14.
 1959 *Neoprioniodus scitulus* (Branson & Mehl) Elias : 151, Pl. 2, figs. 6, 7.
 1959 *Neoprioniodus cassilaris* (Branson & Mehl) Elias : 153, Pl. 2, figs. 20, 21 only.
 1961 *Neoprioniodus scitulus* (Branson & Mehl) Higgins : 220, Pl. 11, fig. 1.
 1961 *Neoprioniodus scitulus* (Branson & Mehl) Rexroad & Burton : 1155, Pl. 140, figs. 15-17.
 1963 *Neoprioniodus scitulus* (Branson & Mehl) Bouckaert & Higgins : 17, fig. 3.
 1963 *Neoprioniodus scitulus* (Branson & Mehl) Thompson & Goebel : 12, fig. 3.
 1964 *Neoprioniodus scitulus* (Branson & Mehl) Rexroad & Furnish : 674, Pl. 111, figs. 36, 37.
 1965 *Neoprioniodus scitulus* (Branson & Mehl) Rexroad & Nicoll : 23, 24, Pl. 2, figs. 21, 22.
Neoprioniodus scitulus (Branson & Mehl) Collinson & Druce (in press), Pl. 2, fig. 1.

MATERIAL. 24 specimens : figured, X 276, X 277, X 278.

RANGE. North Crop 3D 2-3D 14/15.

DESCRIPTION. This is a variable species which, as Rexroad (1958 : 23) has demonstrated, shows appreciable variation during ontogeny in the relative curvature of the anterior denticle, the length of the aboral projection and the outline of the aboral margin. The basal cavity is also variable, and tends to be filled in during growth, ultimately resulting in a minute pit, with a longitudinal median groove extending anteriorly and posteriorly from it. There are also smaller differences in the form and denticulation of the posterior bar, which are shown by numbers of well-preserved specimens in the present faunas. In younger individuals the posterior inclination of the denticles of the posterior bar tends to be correspondingly greater than that in older individuals, but this, as well as the other variations, seem to fall within the limits of Branson & Mehl's species.

REMARKS. The variation in "another prioniodid" mentioned by Branson & Mehl (1940 : 174) as including a minute pit and attachment scars on the lateral faces of the anterior denticle, seem to fall within the variation of the present species, rather than representing a distinct species as they suggest. The most striking general features of the present species are the long slender elegant anterior denticle, the rather short finely pointed aboral process, and the relatively slender, straight to slightly curved posterior bar, together with a general lack of flaring in the lateral faces below the anterior denticle.

Neoprioniodus spathatus Higgins

Plate 21, figs. 9a, b

- 1961 *Neoprioniodus spathatus* Higgins : 217, Pl. 11, figs. 2, 4, text-fig. 5.

MATERIAL. 1 specimen : figured, X 279.

RANGE. North Crop 3D 14/15.

DESCRIPTION. The diagnostic feature of this species is the spatulate plough-like form of the aboral process, which projects with conspicuously concave lateral faces and strongly laterally extended basal surfaces. It has a denticulated anterior edge.

The anterior denticle is relatively strongly developed. Its inner lateral face is flat to very feebly convex, but its outer lateral face is more strongly convex. It has very sharp anterior and posterior edges and is laterally twisted and slightly inwardly

recurved in its upper portion. In inner lateral view, it is concave in its anterior proximal portion and feebly convex in its posterior proximal portion. It is elongated and more or less sharply pointed, the anterior and posterior edges being straight. The aboral process is strongly developed, with a concave to straight anterior margin, and a continuously convex posterior margin. Its lateral faces are flat in the anterior portion, but the base of the inner lateral side is strongly flared to give a conspicuously spatulate appearance. Its anterior edge has 2 or 3 minute denticles developed on it which are of smaller size than any on the posterior bar.

The posterior bar is short and relatively deep. It bears more than 6 denticles, which are more or less erect or only slightly posteriorly inclined to the bar, and which are discrete for at least half their length. They are regularly pointed and have feebly convex lateral faces and sharp anterior and posterior edges. In outer lateral view the whole unit is conspicuously bowed inwards. In aboral view the most conspicuous feature is a continuous slit-like groove, which runs to the anterior aboral point of the anterior aboral process and along its mid-line, being continued as a narrowing slit along the posterior bar.

The posterior bar is much thinner than the aboral process but the basal groove is not conspicuously expanded below the process. It is, however, slightly wider behind the posterior part than it is below the anterior. The lateral aboral faces of the aboral process are more or less straight in aboral view, the basal margin being widest below the posterior end of the process and then curving inward sharply towards the posterior bar. The aboral faces are more or less flat.

REMARKS. Collinson & Druce (in press) include this species as a junior synonym of *N. singularis* (Hass). We have only a single specimen in our collections and we are not in a position to determine the range of morphological variation.

Neoprioniodus tulensis (Pander)

Plate 21, figs. 19a, b

- 1856 *Prioniodus tulensis* Pander (*partim*) : 30, Pl. 2a, fig. 1 only.
 1928 *Prioniodus tulensis* Pander ; Holmes (*partim*) : 22, Pl. 3, fig. 18 only.
 1940 *Prioniodus cassilaris* Branson & Mehl : 186, Pl. 6, figs. 11, 12, 15, 17.
 1950 *Prioniodus cassilaris* Branson & Mehl ; Youngquist, Miller & Downs : 528, Pl. 67, figs. 23, 24.
 non 1957 *Prioniodina cassilaris* (Branson & Mehl) Bischoff : 47, Pl. 5, figs. 38, 39 (= *N. peracutus*).
 1963 *Neoprioniodus tulensis* (Pander) Rexroad & Collinson : 18, Pl. 2, fig. 17, 22, 23.

MATERIAL. 5 specimens : figured, X 280.

RANGE. North Crop CYD 6-CYD 7.

DESCRIPTION. The distinctive feature of the present specimens is the long, recurved, bluntly pointed anterior denticle, the broad spatulate form of the aboral process, and the elongated posterior bar, which bears a series of about 15 denticles on its oral surface. These denticles are discrete for most of their length, and decrease in size posteriorly.

The anterior denticle is elongated, wide and bluntly pointed. It is gently recurved in its distal half, but its proximal half stands only slightly inclined to the anterior portion of the posterior bar. It has sharp anterior and posterior edges and very feebly convex lateral faces, the outer distal lateral face being almost flat.

The aboral process is broad in relation to its length. Its anterior edge is a continuation of the anterior edge of the anterior denticle, and it is more or less straight. Its anterior aboral termination is bluntly rounded and its posterior aboral edge is strongly convex. It has flat lateral faces.

The posterior bar is elongated, and has a concave proximal portion and a relatively straight distal portion when seen in outer lateral view. It decreases in depth posteriorly and bears about 15 denticles; those of the median third tend to be the largest and they decrease posteriorly in size; they are basally confluent but are discrete for most of their length, with sharp anterior and posterior edges and gently convex lateral faces. There is a tendency in the median part of the bar for a hindeodellid type of denticulation, but this is not a conspicuous feature of the unit. The outer lateral face of the posterior bar is flat and shows a very slight bevelled ridge parallel to its aboral surface. The whole unit is gently incurved in a horizontal plane, so that its inner lateral face is concave. The denticles of the posterior bar stand more or less erect to the bar itself.

In inner lateral view the anterior denticle is much more strongly curved and the curvature is especially strongly developed on the posterior proximal lateral face. The inner aboral longitudinal edge of both the aboral process and the posterior bar are sharply bevelled and the inner lateral curvature of both the anterior denticle and the posterior bar are conspicuous.

The aboral surface is marked by a shallow pit below the anterior denticle, which is extended posteriorly as a very narrow slit-like cavity. The basal cavity also extends anteriorly as a narrow slit-like process, running along the median part of the anterior aboral surface. The basal cavity itself is not conspicuously laterally expanded. There is a strong bevelled flange on the inner aboral edge of the anterior aboral process. The strongest lateral curvature of the posterior bar occurs in its anterior half, the posterior part being more or less straight.

REMARKS. The only substantial difference between the present species and *N. scitulus* (Branson & Mehl) is the longer posterior bar of the present specimens, which bears a greater number of denticles. There seems to be a morphological discontinuity between the two, but we are not certain about this and further study may indicate that the two are morphologically continuous and that *N. scitulus* should be regarded as a junior synonym of *N. tulensis*.

Neoprioniodus varians (Branson & Mehl)

Plate 21, figs. 18a, b

1940 *Prioniodus varians* Branson & Mehl : 174, Pl. 5, figs. 7, 8.

1941 *Prioniodus barbatus* Branson & Mehl ; Ellison & Graves : 3, 4, Pl. 1, fig. 27 only.

1957 *Prioniodina varians* (Branson & Mehl) Bischoff : 49, Pl. 5, fig. 35.

1957 *Prioniodina varians* (Branson & Mehl) Ziegler in Flügel & Ziegler : 50.

- 1957 *Neoprioniodus varians* (Branson & Mehl) Rexroad : 35, Pl. 2, fig. 10.
 1958 *Neoprioniodus varians* (Branson & Mehl) Rexroad : 24, Pl. 5, figs. 3, 4.
 1961 *Neoprioniodus varians* (Branson & Mehl) Rexroad & Burton : 1155, Pl. 140, figs. 9, 10.
 1965 *Neoprioniodus varians* (Branson & Mehl) Rexroad & Nicoll : 24, Pl. 2, fig. 18.

MATERIAL. 7 specimens : figured, X 281.

RANGE. North Crop CYD 7-3D 17.

DESCRIPTION. The present specimens have a conspicuous and relatively short anterior denticle, which is very wide at its base in comparison with its length. It is regularly tapered, its anterior and posterior edges being straight, and its distal tip pointed. Its inner lateral face is strongly convex in the proximal portion and less strongly convex in the distal portion. It is extended aborally as a very short aboral process, with a straight anterior edge and a continuously concave posterior edge, which is continuous with the concave margin of the posterior bar when viewed in lateral view. Its inner lateral face is only feebly convex, and there is no sharp inner basal flexure.

The posterior bar, when seen in inner lateral view, is continuously and relatively strongly curved downward. It decreases in depth posteriorly and its posterior aboral corner is bluntly rounded. Its lateral face is strongly convex in the anterior half, but flat to feebly convex in the posterior part, its basal margin being slightly bevelled. Its oral surface bears about 16 large denticles, between which there are some smaller "germ" denticles developed, especially in the anterior third. The denticles as a whole are closely crowded, but the major denticles are generally not confluent with one another. The denticles in the median half of the bar tend to be rather larger in size than the rest. The denticles on the posterior quarter of the bar are the smallest. All the denticles stand more or less erect to the basal surface below them, and have sharp anterior and posterior edges and convex lateral faces. They are short and bluntly pointed.

The anterior denticle stands erect to the oral surface of the posterior bar in contact with it. It is also gently curved inward along its length.

In outer lateral view, there is a very conspicuous bevelled edge along the whole of the aboral margin. The outer lateral face of the anterior denticle and the aboral process is more or less flat in the lower proximal portion, but becomes gently convex in the distal two-thirds. The curvature of the posterior bar is very conspicuous, and the bar decreases in depth posteriorly. In lateral view the anterior end of the aboral process is slightly flexed outward in a horizontal plane, and the main part of the posterior bar is gently flexed inward, so that its inner lateral face is concave. There is a deep and obvious basal cavity below the posterior part of the anterior denticle, which decreases in width but is continued as a rather wide extension along both the aboral process and the posterior bar.

Neoprioniodus sp. nov. A

Plate 22, fig. 14

MATERIAL. 1 specimen : figured, X 282.

RANGE. North Crop 3D 17.

DESCRIPTION. This species is marked by the lack of a large aboral process and the presence of a wide flaring basal cavity. The anterior denticle is strongly laterally compressed, fairly short and recurved in its aboral third. The posterior bar is deep and relatively short, bearing a series of 14 fused, laterally compressed, needle-like denticles, which are inclined posteriorly. In aboral view the pit is large and sub-apical, having flaring lips. It runs along the posterior bar as a narrowing cavity terminating at the posterior extremity of the posterior bar.

Neoprioniodus cf. *armatus* (Hinde)

Plate 21, figs. 3a-c

1879 *Prioniodus armatus* Hinde (*partim*) : 360, Pl. 15, fig. 20, non fig. 21.

MATERIAL. 3 specimens : figured, X 283.

RANGE. North Crop ZLA 14.

DESCRIPTION. The anterior denticle is tall and laterally compressed. The anterior edge is feebly concave in lateral view, with a sharp anterior and posterior edge. The blunt aboral surface projects slightly aborally. The posterior bar is denticulate, curved inward, and slightly twisted. The fused denticles are small, more or less erect, number about 11, and decrease in height posteriorly. The cavity is small and situated postero-aborally of the anterior denticle.

REMARKS. This form appears to be very close to *Neoprioniodus armatus* (Hinde 1879, Pl. 15, fig. 20) which is most abundant in the Upper Devonian. This species probably has a long range, and the present specimens may well belong to it but because of their limited occurrence, both stratigraphically and numerically, we have not made a direct assignation. Hinde's fig. 21 probably represents a different species.

Neoprioniodus cf. *camurus* Rexroad

Plate 22, figs. 1a-4b

1957 *Neoprioniodus camurus* Rexroad : 33, Pl. 2, figs. 18-20.

MATERIAL. 10 specimens : figured, X 284, X 285, X 286, X 287.

RANGE. North Crop 3D 14/15.

DESCRIPTION. The distinctive features of this species are the relatively elongated posterior bar, the sharp inner lateral curvature of the bar immediately posterior to the anterior denticle, and the slender anterior denticle and aboral process.

The posterior bar is more or less straight in inner lateral view, and is relatively shallow. Its oral surface bears up to 18 denticles, some of which are separated by smaller germ denticles. The denticles are confluent for most of their length, and only their apices are discrete. The apices are sharply pointed with sharp anterior and posterior edges and gently convex lateral faces ; those in the posterior quarter

stand more or less erect to the basal surface of the bar, but those in the anterior three-quarters are inclined slightly anteriorly. The denticles are of variable height but there is no conspicuous increase or decrease in height in either direction. There is a slight tendency for the two denticles immediately posterior to the anterior denticle to be larger than the rest. The anterior denticle, which is not conspicuously large, is flexed sharply inwards, so that its inner lateral edge points inwardly and anteriorly, making an angle of about 140° with the posterior bar. When seen in inner lateral view, looking directly at the junction between the anterior denticle and the posterior bar, the angle between the posterior edge of the aboral process and the posterior bar is about 70° . The anterior denticle is more or less straight, with sharp and straight anterior and posterior edges and gently convex lateral faces.

The aboral process is relatively short in comparison with the length of the denticles, with a rather sharp aboral point, and straight anterior and posterior edges.

In outer lateral view the most conspicuous feature of the unit is the sharp lateral recurvature at a point about two or three denticles posterior to the anterior denticle. There is a faintly perceptible longitudinal bevelled edge developed, but the whole aboral surface of the unit is rather thin, although it is excavated by a longitudinal slit. There is a shallow, little-flared, posterior cavity below the posterior margin of the anterior denticle.

Genus *OZARKODINA* Branson & Mehl 1933

1933 *Ozarkodina* Branson & Mehl 51.

TYPE SPECIES. *Ozarkodina typica* Branson & Mehl.

Ozarkodina curvata Rexroad

Plate 27, fig. 6

1958 *Ozarkodina curvata* Rexroad : 24, Pl. 4, figs. 1-3.

1961 *Ozarkodina curvata* Rexroad ; Rexroad & Burton : 1156, Pl. 141, figs. 13, 14.

1964 *Ozarkodina curvata* Rexroad ; Rexroad & Furnish : 674, Pl. 111, figs. 10, 11.

1965 *Ozarkodina curvata* Rexroad ; Rexroad & Nicoll : 25, Pl. 2, figs. 1, 2.

Ozarkodina curvata Rexroad ; Collinson & Druce (in press).

MATERIAL. 1 specimen : figured, X 289.

RANGE. North Crop CYD 7.

DESCRIPTION. The most conspicuous feature of this species is the short, strongly depressed anterior bar, which bears a series of about 4 denticles on its oral edge. These are basally confluent, and only their apices are discrete, being sharply pointed, with gently convex lateral faces. They tend to be recurved parallel to the apical denticle, and show a more or less constant decrease in size anteriorly, those adjacent to the apical denticle being the largest. The anterior bar is relatively deep and relatively straight ; its anterior end is bluntly spatulate and its outer lateral face more or less flat. There is a rather flat bevel visible along the whole aboral edge of the unit, when seen in outer lateral view. The base of the apical denticle is about

two to three times as wide as the largest denticles adjacent to it, and is confluent with them. It is recurved posteriorly but has a more or less straight posterior edge and is bluntly pointed. It has sharp anterior and posterior edges. Its outer lateral face is feebly convex, and the basal margin is sharply, but not greatly, outflexed below it to give a rather inconspicuous navel. The posterior bar is about twice the length of the anterior, but is less deep. It is straight along its aboral margin and the distal end makes an angle of about 90° with the distal end of the anterior bar. The posterior bar decreases in depth posteriorly and bears a series of crowded confluent denticles, more or less of similar size. These number up to about 11 or 12, and have rather sharply pointed free tips. They show no overall trend in size, but the posterior ones tend to be slightly smaller than the rest. Germ denticles are visible between some of them. Those near the anterior end of the posterior bar tend to be inclined posteriorly, but those towards the distal end of the bar stand more or less erect to the base of the bar itself. The whole posterior bar is sharply inflexed at about its mid-length, so that its inner lateral face is longitudinally concave. The posterior aboral corner of the unit is sharply rounded. In inner lateral view, the inward curvature of the unit is a very conspicuous feature.

There is a small basal cavity below the posterior edge of the denticle, around which the basal margins flare slightly. This is continued as a conspicuous but narrow slit along the anterior and posterior bars.

Ozarkodina compressa Rexroad

Plate 27, fig. 23

- 1957 *Ozarkodina compressa* Rexroad : 36, Pl. 2, figs. 1, 2.
 1958 *Ozarkodina compressa* Rexroad ; Rexroad : 24, Pl. 6, figs. 1, 2.
 1961 *Ozarkodina compressa* Rexroad ; Rexroad & Burton : 1156, Pl. 141, figs. 16, 17.
 1964 *Ozarkodina compressa* Rexroad ; Rexroad & Furnish : 674, Pl. 111, fig. 9.
 1965 *Ozarkodina compressa* Rexroad ; Rexroad & Nicoll : 24, 25, Pl. 2, figs. 3, 4.

MATERIAL. 12 specimens : figured, X 420.

RANGE. Avon Gorge C 3-S 49, North Crop 3D 14/15-3D 22.

DESCRIPTION. The present specimens are broadly similar to those described by Rexroad and other authors, although they differ slightly in that the posterior bar

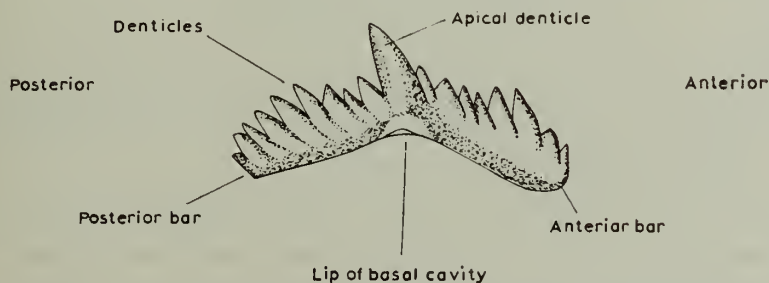


FIG. 33. *Ozarkodina* sp. showing morphological terms used in the text.

tends to be rather more elongate and is slightly twisted. This distinction does not seem sufficient, however, to warrant their recognition as a different species, and in other aspects of their denticulation and general form they closely resemble *Ozarkodina compressa*.

Ozarkodina delicatula (Stauffer & Plummer)

Plate 27, figs. 15, 19

- 1932 *Bryantodus delicatulus* Stauffer & Plummer : 29, Pl. 2, fig. 27.
 1932 *Bryantodus nasutus* Stauffer & Plummer : 29, Pl. 2, fig. 28.
 1932 *Bryantodus sulcatus* Stauffer & Plummer : 30, Pl. 2, figs. 11, 14, 30.
 1933 *Bryantodus delicatus* Gunnell : 267, Pl. 32, fig. 43.
 1933 *Bryantodus rugosus* Gunnell : 269, Pl. 32, fig. 44.
 1933 *Bryantodus stritatus* Gunnell : 268, Pl. 32, fig. 45.
 1933 *Bryantodus strigillatus* Gunnell : 268, Pl. 32, fig. 46.
 non 1933 *Bryantodus delicatus* (Stauffer & Plummer) Branson & Mehl : 222, Pl. 16, fig. 19.
 1941 *Ozarkodina delicatula* (Stauffer & Plummer) Ellison : 120, Pl. 20, figs. 40-42, 47.
 1941 *Ozarkodina delicatula* (Stauffer & Plummer) Ellison & Graves : 3, Pl. 1, figs. 12-14.
 1944 *Ozarkodina delicatula* (Stauffer & Plummer) E. B. Branson : 327.
 1948 *Ozarkodina delicatula* (Stauffer & Plummer) Youngquist & Heezen : 771, Pl. 118, fig. 6.
 1949 *Ozarkodina delicatula* (Stauffer & Plummer) Youngquist & Downs : 168, Pl. 30, figs. 1, 3, 7, 11.
 non 1949 *Bryantodus delicatus* (Stauffer & Plummer) Beckmann 161, Pl. 1, fig. 7 ; Pl. 3, fig. 3.
 1952 *Ozarkodina delicatula* (Stauffer & Plummer) Rhodes : 893, Pl. 126, figs. 2, 3.
 1957 *Ozarkodina delicatula* (Stauffer & Plummer) Bischoff : 39, Pl. 1, figs. 25-28.
 1958 *Ozarkodina compressa* Rexroad (*partim*) : 24.
 1961 *Ozarkodina delicatula* (Stauffer & Plummer) Higgins : 220, Pl. 12, fig. 13.
 1961 *Ozarkodina delicatula* (Stauffer & Plummer) Rexroad & Burton : 1156, Pl. 141, fig. 12.
 1963 *Ozarkodina delicatula* (Stauffer & Plummer) Bouckaert & Higgins : 17, fig. 3.
Ozarkodina delicatula (Stauffer & Plummer) Collinson & Druce (in press).

MATERIAL. 27 specimens : figured, X 290, X 291.

RANGE. North Crop CYD 7-3D 20.

DESCRIPTION. This is a relatively variable species with the following characteristics. Anterior and posterior bars are thin, blade-like, straight or continuously gently arched, the anterior tending to be the deeper and the longer. Denticles closely spaced, more or less sub-equal, discrete only at their pointed apical ends. Apical denticle is from one and a half to three times the width of the adjacent denticles. It has a slightly flared basal cavity.

The anterior bar is of more or less uniform depth and has a straight to gently concave aboral edge. It bears 12 to 14, strongly laterally compressed denticles, which are confluent for most of their length only their apical tips being discrete. These are sharply pointed, with sharp anterior and posterior edges which are straight. The anterior bar itself is about equal in depth to the length of the denticles. The

denticles at the anterior end of the bar are more or less erect, but those toward the posterior end become increasingly strongly inclined posteriorly. In a few specimens the denticles at the anterior end of the bar are also posteriorly inclined. The lateral faces of the anterior bar are flat to gently convex, the convexity increasing in the posterior half of the bar. The apical denticle is variable in size and in inclination. It is of similar form to the denticles of the anterior bar and its free portion is sharply pointed, with sharp, straight anterior and posterior edges. It is strongly inclined at an angle of up to about 50° to the posterior bar, and is from one and a half to three times as wide and about twice as long as the largest adjacent denticles. In some specimens the denticles of the anterior bar are more widely spaced and appear almost discrete, but in most specimens they are more or less confluent.

The posterior bar is depressed with respect to the anterior, and the whole aboral surface is either continuously and gently concave, or both the anterior and posterior bars may be more or less straight and meet at an angle of about 120° . (This is the projected angle made by their straight distal ends in those specimens where the lower surface is strongly arched). The posterior bar bears 10 or more laterally compressed closely spaced denticles, which, although in some specimens they are more or less equal in size, show a marked decrease in size in the posterior quarter of the bar in others. They are generally rather smaller than the denticles of the anterior bar and fewer in number. In some specimens the posterior bar, and to a lesser extent the anterior bar, are strongly flexed inwards. The denticles of the posterior bar are all inclined at about 50° to the posterior bar itself.

In aboral view the unit has a rather conspicuously flattened aboral margin, which decreases in width towards the anterior and posterior ends of the unit. There is a continuous longitudinal slit along both limbs, and a slightly flared median cavity below the apical denticle, which is continuous with the slit. The flaring of this cavity is not a conspicuous feature, but the thickened lips of the main longitudinal cavity are more or less conspicuous in aboral view.

This species shows some variation in the degree of flexing of the anterior and posterior bars in a vertical plane and in the relative depth and detailed denticulation of the anterior bar. Specimens illustrating various morphological variations are illustrated.

Ozarkodina hindei Clarke

Plate, 27 figs. 16, 17, 22

- 1879 *Polygnathus dubius* Hinde : 363, Pl. 16, fig. 8 only.
 1900 *Polygnathus dubius* Hinde ; Hinde : 341, Pl. 9, fig. 1 only.
 1928 *Prioniodina (Polygnathus) dubius* (Hinde) Holmes : 19, Pl. 8, fig. 1 only.
 1960 *Ozarkodina hindei* Clarke : 18, Pl. 3, figs. 1, 6.
 1961 *Ozarkodina compressa* Rexroad ; Rexroad & Burton : Pl. 141, fig. 16 only.

MATERIAL. 3 specimens : figured, X 294, X 293, X 295.

RANGE. North Crop 3D 6-3D 12.

DESCRIPTION. The diagnostic features of this species are the very deep and strongly laterally compressed anterior and posterior bars, and the very wide, short

and conspicuously pointed apical denticle. The anterior bar is deeper than the posterior, and carries from 4 to 6 denticles on its oral edge. These are very strongly laterally compressed and more or less sharply recurved, being confluent for the greater part of their length. Their apical halves are discrete, and they are sharply pointed with straight anterior and posterior edges, the anterior edge tending to be sharply deflected at an angle of about 130° at or near the point of confluence with the adjacent denticles, but the posterior edge being straight throughout its length. Germ denticles are visible in places on the anterior bar, especially at its junction with the apical denticle. The most posterior denticle of the apical bar is so coalesced with the anterior edge of the apical denticle that only its highest portion is discrete. The anterior bar tends to show a slight increase in depth anteriorly; the denticles in the posterior two thirds of the bar are of more or less uniform height. There may, however, be 1 or 2 much smaller blunt denticles present on the spatulate anterior end. The denticles may curve slightly inwardly in some specimens. The inner lateral face of the anterior bar is more or less flat, but the outer lateral face has a conspicuous, shoulder-like thickening near the base of the denticles. The anterior bar tapers sharply towards the aboral margin.

The apical denticle is at least three times as wide as the largest denticles of the anterior and posterior bars. It is very sharply pointed, and is only about twice as long as its basal width. It is recurved posteriorly at an angle of about 60° to the posterior bar, and germ denticles are conspicuous at its base. There is a feebly flaring protrusion of the basal margin below its posterior margin.

The posterior bar is shorter and shallower than the anterior, and bears up to 9 denticles of more or less uniform height, basally confluent, but their apices discrete and sharply pointed. They tend to be very slightly smaller than those of the larger series of the anterior bar. The posterior bar thickens towards its aboral surface, which is wide and flat, as an extension of the basal cavity below the apical denticle. It decreases in both width and depth posteriorly, however, and its posterior aboral margin is bluntly rounded. Its inner lateral face is more or less flat and the posterior denticles are gently inclined to the base of the posterior bar. The posterior bar and the anterior bar have relatively straight aboral margins and they make an angle of about 130° with one another in a vertical plane.

The whole unit is strongly bowed laterally in a horizontal plane so that it is concave on the inner side, and the denticles are also incurved to a varying degree. This is especially true of the apical denticle. The anterior edge of the anterior bar has an acute angle at the anterior aboral margin and is inclined sharply posteriorly, with a faintly serrated anterior edge in some specimens. In outer lateral view the lateral faces of the unit are flat to gently convex, and the inner curvature is a conspicuous feature. In most specimens there is developed to a varying intensity a bevelled aboral margin, especially conspicuous in the median half of the unit, which includes the posterior part of the anterior bar and the anterior part of the posterior bar. The outer lateral view of the navel below the posterior edge of the apical denticle is distinct and forms a rather flattened apical area.

In aboral and outer lateral views the basal cavity is a conspicuous feature, partic-

ularly so in outer view. There is a strong basal expansion below the posterior edge of the apical denticle, and in the anterior third of this, the basal cavity is deepest and widest, forming a biconvex pit. It is extended anteriorly and posteriorly as a shallow slit-like groove, but the posterior extension becomes indistinct near the posterior end of the margin of the expanded base. The anterior extension continues towards but does not quite reach the anterior end of the anterior blade.

REMARKS. This species is close to *O. compressa* Rexroad, but differs from it in the shorter and deeper anterior and posterior bars and the short and relatively very broad apical denticle.

Ozarkodina macer (Branson & Mehl)

Plate 27, figs. 7, 8

- 1934 *Bryantodus macer* Branson & Mehl : 283, Pl. 23, fig. 4.
 1934 *Ozarkodina elongata* E. R. Branson : 313, Pl. 28, fig. 25.
 ? 1934 *Bryantodus scitulus* Branson & Mehl : 283, Pl. 23, fig. 5.
 1943 *Bryantodus equalis* Cooper in Cooper & Sloss : 170, Pl. 29, fig. 9.
 1943 *Bryantodus* cf. *planus* Branson & Mehl ; Cooper in Cooper & Sloss : 170, Pl. 29, fig. 3.
 1943 *Ozarkodina regularis* Branson & Mehl ; Cooper in Cooper & Sloss : 170, Pl. 29, fig. 12.
 1943 *Subbryantodus grandis* Cooper in Cooper & Sloss : 175, Pl. 29, fig. 19.
 1949 *Ozarkodina* cf. *elongata* Branson & Mehl ; Thomas : 411, Pl. 4, fig. 28.
 1955 *Ozarkodina regularis* Branson & Mehl ; Sannemann : 133, Pl. 6, fig. 5 only.
 1957 *Ozarkodina willsi* Rhodes & Dineley : 364, Pl. 38, figs. 1, 5.
 1957 *Ozarkodina firma* (Stauffer) Rhodes & Dineley : 364, Pl. 27, fig. 20.
 1957 *Ozarkodina delicatula* (Stauffer & Plummer) Bischoff : 39, Pl. 1, figs. 25-28.
 1957 *Ozarkodina roundyi* (Hass) Bischoff : 40, Pl. 2, fig. 2 only.
 1957 *Ozarkodina congesta* Stauffer, Bischoff & Ziegler : 75, 76, Pl. 12, figs. 18-20, Pl. 13, fig. 14.
 1958 *Ozarkodina tortilis* Tatge ; Huckriede : 154, Pl. 11, fig. 26 only.
 1959 *Ozarkodina* cf. *delicatula* (Stauffer & Plummer) Helms : 646, Pl. VI, figs. 14-16.
 1959 *Ozarkodina* cf. *regularis* Branson & Mehl ; Helms : 647, Pl. IV, figs. 13, 14, (*non* Pl. IV, fig. 15=*O.* cf. *congesta*).
 1960 *Ozarkodina regularis* Branson & Mehl ; Zimmermann : Pl. IX, fig. 11 only.
 1960 *Ozarkodina media* Walliser ; Spasov : 68, Pl. 1, fig. 10 only.

MATERIAL. 71 specimens : figured, X 304, X 305.

RANGE. Avon Gorge K 8-Z 38.

DESCRIPTION. A gently arched blade with asymmetrical anterior and posterior blades, commonly bearing 5 to 7 straight, posteriorly inclined denticles on the anterior blade, and 8 to 12 straight posteriorly inclined denticles on the posterior blade. The denticles of the anterior and posterior blades may be of uniform elevation, highest near the apical denticle and decreasing in elevation to the extremities of the blades, or they may be of variable elevation. The apical denticle is straight to slightly curved, posteriorly inclined and higher and wider than the blade denticles. The small circular basal cavity is situated beneath the apical denticle. The aboral edge is sharp.

REMARKS. *Ozarkodina macer* (Branson & Mehl) as here defined, includes a group of ozarkodinids which are characterized by having asymmetrical anterior and posterior limbs. The outline of the denticles of both the anterior and posterior blades is similar in lateral view. *O. macer* resembles *O. cf. congesta* in the outline of the blades in lateral view, but in *O. macer* the anterior and posterior limbs are asymmetrical whereas in *O. cf. congesta* they are symmetrical.

Compared with *Ozarkodina macra* the blade of *Ozarkodina macer* is thinner.

Ozarkodina macra Branson & Mehl

Plate 27, figs. 12, 20, 21

- ? 1931 *Bryantodus equalis* Cooper : 234, Pl. 28, fig. 9.
 ? 1931 *Bryantodus subequalis* Cooper : 234, Pl. 28, fig. 11.
 1934 *Ozarkodina macra* Branson & Mehl : 192, Pl. 17, fig. 5.
 1934 *Ozarkodina regularis* Branson & Mehl : 287, Pl. 23, figs. 13, 14.
 ? 1938 *Ctenognathus firmus* Stauffer : 425, Pl. 48, figs. 2, 6, 15.
 1955 *Ozarkodina regularis* Branson & Mehl ; Sannemann : 133, Pl. 6, figs. 3, 7 only.
 ? 1956 *Ozarkodina rhenana* Bischoff & Ziegler : 153, Pl. 14, fig. 19.
 ? 1957 *Ozarkodina ballai* Bischoff & Ziegler : 74-75, Pl. 13, figs. 1, 2.
 1957 *Ozarkodina macra* Branson & Mehl ; Bischoff & Ziegler : 77, Pl. 12, figs. 13a, b, Pl. 13, figs. 10a, b.
 1957 *Ozarkodina cf. macra* Branson & Mehl ; Bischoff & Ziegler : 78, Pl. 13, fig. 11, Pl. 19, fig. 43.

MATERIAL. 36 specimens : figured, X 296, X 298, X 297.

RANGE. Avon Gorge K 2-Z 18, North Crop KL 2-KL 16.

DESCRIPTION. The aboral edge in lateral view is slightly arched. The anterior and posterior blades are of almost equal length, and bear 8-12 straight, posteriorly inclined denticles, fused for the greater part of their length but free at their tips. The anterior blade is thicker than the posterior blade. The apical denticle is two to three times as wide as the denticles of the anterior and posterior blade. It is inclined to the posterior at an angle of 70°. The small circular basal cavity is situated immediately beneath the apical denticle and the aboral edge is sharp.

Ozarkodina parva (Huddle)

Plate 27, fig. 18

- 1934 *Bryantodus parvus* Huddle : 74, 75, Pl. 4, fig. 9.
 1939 *Bryantodus orthus* Cooper : 385, Pl. 43, figs. 33, 34.
 1939 *Subbryantodus ? scitulus* (Branson & Mehl) Cooper : 417, Pl. 43, figs. 35, 36.

MATERIAL. 107 specimens : figured, X 299.

RANGE. Avon Gorge K 3-C 7, North Crop KL 2-ZLA 32.

DESCRIPTION. The blade is short, thin, symmetrical and slightly arched. The apical denticle is subcentral, flattened, sharp edged and acutely pointed to the posterior. The blade denticles are closely appressed and similar to the apical denticle in outline, inclination and insertion. They number 7 to 12 on each side of the apical

denticle, are fused for the greater part of their length, and are highest near the apical denticle. They decrease in height uniformly to the anterior and posterior extremities. The basal cavity is small and thin, and is situated beneath the apical denticle.

***Ozarkodina plana* (Huddle)**

Plate 27, figs. 1-3

- 1934 *Bryantodus planus* Huddle : 75-76, Pl. 10, fig. 8.
 non 1934 *Bryantodus planus* Huddle ; Branson & Mehl : 284, Pl. 23, fig. 8.
 1957 *Ozarkodina* cf. *O. plana* (Huddle) Rhodes & Dineley : 364, Pl. 37, fig. 24.
 1961 *Ozarkodina plana* (Huddle) Scott & Collinson : 128, Pl. 2, fig. 8.

MATERIAL. 12 specimens : figured, X 300, X 301, X 419.

RANGE. Avon Gorge K 3-Z 15.

DESCRIPTION. The anterior and posterior blades are short, slightly arched, laterally compressed, and very thin. The apical denticle is short, broad at the base, acutely pointed and situated slightly anterior to the basal cavity. The blade denticles are similar in outline to the apical denticle and usually number 4 anteriorly and 6 posteriorly. The basal cavity is small and situated slightly anterior to the apical denticle.

***Ozarkodina plumula* Collinson & Druce**

Plate 27, figs. 4, 5

Ozarkodina plumula Collinson & Druce (in press).

MATERIAL. 4 specimens : figured, X 302, X 303.

RANGE. North Crop 3D 12.

DESCRIPTION. The diagnostic characteristic of this species is the slender elongated anterior bar, bearing a large number of small, posteriorly inclined denticles. The posterior bar is shorter and deeper, and bears a smaller number of conspicuously larger denticles than those of the anterior bar. The apical denticle is only slightly larger than the largest of the posterior bar and the whole unit is more or less continuously recurved. The anterior bar is of slender elongate construction, relatively shallow in depth, and bears a series of up to 12 small confluent denticles, only the apical tips of which are discrete. These are sharply inclined to the anterior bar and tend to decrease in size posteriorly.

The apical denticle is only slightly larger than those adjacent to it both in length and in width. It is, however, conspicuously more sharply inclined than most of those of the anterior bar, and in this it parallels the denticles of the shorter posterior bar. It is very strongly laterally compressed, with sharp anterior and posterior edges, and is confluent with the posterior denticles for the greater part of its posterior margin, though its inclination removes most of its anterior edge on the adjacent anterior denticles.

The denticles of the posterior bar are similar to, but rather larger than, those of the

anterior. They are about 5 or 6 in number and are strongly laterally compressed with sharp anterior and posterior edges and gently biconvex lateral faces. Their bases are confluent and their sharply pointed apices discrete. The posterior bar is deeper than the anterior, and tends to become shallower towards its posterior end. It is inclined to the anterior bar at an angle which varies from 130° – 140° , although the junction between the two is continuously curved, so that the whole aboral margin is concave with more or less straight distal ends.

There is a relatively inconspicuous flare on the basal margin below the posterior edge of the apical denticle. The basal cavity is gently flared, being slightly larger than that of many typical ozarkodinids. It is continued as a longitudinal slit along both the anterior and the posterior bars, both of which become narrower towards the aboral margin. The whole unit is more or less straight in a vertical plane.

In complete specimens the denticles are seen to be sharply pointed, and the denticles of the posterior bar are discrete for a greater part of their length than those of the anterior bar. The posterior aboral corner of the posterior bar is very strongly rounded and terminates orally in the tip of the posterior denticle.

Ozarkodina cf. *congesta* Stauffer

Plate 27, fig. 13

1940 *Ozarkodina congesta* Stauffer : 427, Pl. 59, fig. 12.

1957 *Ozarkodina plana* Huddle ; Bischoff & Ziegler 78, 79, Pl. 12, fig. 15a, b.

1959 *Ozarkodina* cf. *regularis* Branson & Mehl ; Helms : 647, Pl. IV, fig. 15 only.

MATERIAL. 14 specimens : figured, X 288.

RANGE. Avon Gorge Z 17–Z 37.

DESCRIPTION. A gently arched unit with symmetrical anterior and posterior blades, commonly bearing 7 straight posteriorly inclined denticles, highest near the apical denticle, and decreasing in length uniformly to the anterior and posterior extremities of the blades. The apical denticle is straight to slightly curved, posteriorly inclined and higher and wider than the blade denticles. The small circular basal cavity is situated beneath the apical denticle, The aboral edge is sharp.

REMARKS. In the Z beds of the Avon Gorge, specimens of *Ozarkodina* are found, which are neither identical with one another nor with previously described species. Reference to the literature shows that previous workers, for example Helms (1959) and Bischoff & Ziegler (1957), have often assigned specimens in their studies to species where the holotype bears little resemblance to their specimens. In the present study, the majority of the Z bed ozarkodinids have been referred to two general categories ; *O.* cf. *congesta* Stauffer, which has symmetrical anterior and posterior limbs, and *Ozarkodina macer* (Branson & Mehl) which has asymmetrical anterior and posterior limbs.

Ozarkodina cf. *delicatula* (Stauffer & Plummer)

Plate 27, fig. 14

1932 *Bryantodus delicatula* Stauffer & Plummer 29, Pl. 2, fig. 27.

MATERIAL. 12 specimens : figured, X 292.

RANGE. North Crop ZLA 31-ZLA 33.

DESCRIPTION. The unit is bowed and slightly curved. Both bars are long. The anterior bar bears about 8 denticles which are sub-equal, laterally compressed, fused at their bases with free chevron tips, and all are inclined posteriorly. The antero-aboral edge is bluntly spatulate. The apical denticle is largest, fairly short, about twice the size of those of the anterior bar, laterally compressed and inclined posteriorly. The posterior bar is of equal length to the anterior bar, but less deep, and shallows posteriorly. The denticles are similar and about 8 in number. The basal cavity is minute and restricted to the aboral region of the apical denticle with sometimes feebly flaring lips.

REMARKS. Stauffer & Plummer (1932 : 29), described *O. delicatula* from Pennsylvanian strata, and it has been recognized in Upper Viséan and Namurian rocks (Bischoff 1957, Higgins 1961). The present specimens appear to be very similar to the type specimens, and it is possible that the species has an even longer range than previously thought.

Ozarkodina cf. *elegans* (Stauffer)

Plate 27, fig. 24

1938 *Ctenognathus elegans* Stauffer : 425, Pl. 48, figs. 9, 12.1940 *Ctenognathus elegans* Stauffer ; Stauffer : 422, Pl. 59, figs. 3-5, 8.1955 *Ozarkodina elegans* (Stauffer) Sannemann : 133, Pl. 6, fig. 9.1956 *Ozarkodina denckmanni* Ziegler : Pl. 7, figs. 1, 2, Pl. 6, figs. 30, 31.1957 *Ozarkodina elegans* (Stauffer) Bischoff & Ziegler : 76, Pl. 20, figs. 29-33.1958 *Ozarkodina denckmanni* Ziegler ; Bischoff & Sannemann : 99, Pl. 14, figs. 22, 23.1960 *Ozarkodina regularis* Branson & Mehl ; Zimmermann : Pl. IX, fig. 10.1961 *Ozarkodina delicatula* (Stauffer & Plummer) Rexroad & Burton : 1156, Pl. 141, fig. 12.1963 *Ozarkodina media* Walliser ; Spasov & Veselinovic : 246, Pl. 1, fig. 14 only.

MATERIAL. 2 specimens : figured, X 109.

RANGE. Avon Gorge Z 19-Z 37.

DESCRIPTION. The anterior blade bears 11 denticles fused to near their tips. The denticles are straight and inclined to the posterior at an angle of 80°. The posterior blade is straight and only half the height of the anterior blade. It bears up to 12 denticles, which are fused for the greater part of their length, but free at their tips. The denticles of the posterior blade are free for a greater part of their length than those of the anterior blade. The denticles of the posterior blade are straight and inclined to the posterior at an angle of 45°. The aboral edge in lateral view, is gently arched. The apical denticle is straight, slightly higher than the posterior

denticle of the anterior blade, and inclined to the posterior at an angle of 70°. It is also three times the width of the blade denticles. The small circular basal cavity is situated beneath the apical denticle. The aboral edge is sharp.

REMARKS. *Ozarkodina* cf. *elegans*, as interpreted in this study, is characterized by having longer denticles on the anterior blade than on the posterior blade.

Ozarkodina sp.

Plate 27, figs. 9–11

MATERIAL. 93 specimens : figured, X 306, X 307, X 308.

RANGE. Avon Gorge K 2–S 53.

REMARKS. A number of broken specimens which contain part of the anterior, or posterior blades, have been found, but it is impossible to refer them to any species with certainty.

Genus *PATROGNATHUS* gen. nov.

DERIVATION OF NAME. From the Latin *pater*—father.

DIAGNOSIS. Symmetrical platform conodonts, with lanceolate platform and short anterior median blade, generally of five denticles, the most posterior one of which is higher than the others. The platform bears a row of 6 to 9 nodes on either margin, separated by a central trough. The basal cavity is large, extending almost the complete length of the aboral surface of the platform, asymmetrical and laterally flared. A small posterior blade, composed of two denticles, is developed in a few specimens, but there is no carina extending along the platform.

TYPE SPECIES. *Patrognathus variabilis* gen. et. sp. nov.

DESCRIPTION. As for *Patrognathus variabilis* sp. nov.

REMARKS. *Patrognathus* is similar to the previously described genera *Taphrognathus* Branson & Mehl, and *Streptognathodus* Stauffer & Plummer, but has a wider and more flared basal cavity. Rexroad (1958A) considered *Taphrognathus* and *Streptognathodus* to be homoeomorphs, but Lindström (1964: 173) considered *Taphrognathus* to be a synonym of *Streptognathodus*. The present authors believe Rexroad's interpretation to be correct, and regard *Patrognathus* as another broad homoeomorph, which is present at the base of the Tournaisian and possibly in the uppermost Upper Devonian.

Glenister & Crespin (1959) reported *Taphrognathus* from the Upper Devonian strata of the Fitzroy Basin in Australia. The specimens have an anterior blade which is lateral in position and, therefore, appear referable to our new genus *Clydagnathus*. Likewise Conil, Lys & Mauvier (1964) reported, but did not illustrate, *Taphrognathus* sp. from the Tn_{1b}–Tn_{2b} horizons of the Franco-Belgian Province. If the anterior blade is lateral in position, then their specimens should be referred to *Clydagnathus* gen. nov. Glenister & Klapper (1966, Pl. 94, fig. 3) have found specimens of "*Scaphignathus*" in Australia identical to our *Clydagnathus*. In one sample it

occurs 150 ft. below the first appearance of *S. aculeatus*, but in another it occurs with *S. aculeatus* and *Palmatolepis glabra*. Sandberg & Klapper (1967) have also found the genus *Clydagnathus* in several sections in Wyoming and Montana, and the genus *Patrognathus* in the Windy Gap Formation of Wyoming, where it is associated with *S. sulcatus* (see also p. 54)

The Lower Devonian *Eognathodus* Philip differs from *Patrognathus* in the form of the anterior blade, although the genera resemble one another in overall form.

Patrognathus variabilis gen. et sp. nov.

Plate 2, figs. 8a-IIC

DERIVATION OF NAME. From the great variability of this form.

DIAGNOSIS. Elongate, symmetrical form, possessing lanceolate platform and medial blade. Carina absent. Posterior denticle of blade twice as large as other blade denticles. Cavity flared, elongate, covering most of platform. Base of cavity and blade grooved.

MATERIAL. 625 specimens: Holotype X 311, Paratypes X 519, X 309, X 310 (all figured).

TYPE LOCALITY AND HORIZON. Avon Gorge, K Zone. Sample KL2.

RANGE. Avon Gorge Samples K 1-K 17, North Crop Samples KL 1-KL 12.

DESCRIPTION. The unit is symmetrical, the platform being lanceolate and straight to slightly curved. The blade varies in length, but is commonly a little

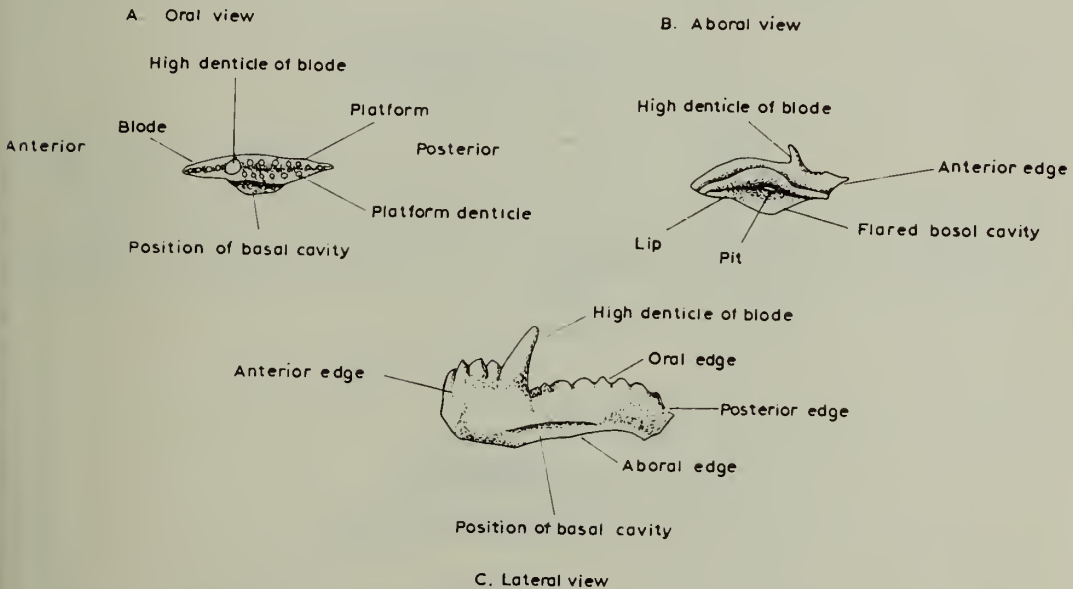


FIG. 34. *Patrognathus* sp. showing morphological terms used in the text.

shorter than the platform. It is situated medially and bears from 4 to 8 denticles, the posterior-most being twice as large as the remainder. There is a general decrease in size anteriorly, and the denticles are more or less erect. The base of the blade is grooved.

Each side of the platform bears a marginal row of laterally elongate nodes, which are transversely paired. These are replaced posteriorly by a single series of medial transverse ridges, composed of two nodes. An additional node is generally developed on the left side of the platform (viewed from the posterior). This additional node, situated at the anterior end of the platform, is developed on the left margin of the platform, irrespective of whether the unit is laterally curved to the right or the left. The number of nodes in each row ranges from 4 to 11. The unit is arched slightly in lateral view and the platform has a nodose edge.

In aboral view the cavity is slightly asymmetrically expanded, the inner half being shorter and more inflated. The base of the cavity is grooved.

REMARKS. Although *P. variabilis* possesses a variable number of nodes on both the blade and platform, calculations of denticle density of both blade and platform and the construction of a scatter diagram of this information, suggest that this variation is continuous (see Fig. 35). The additional node at the anterior of the inner row of lateral nodes on "right" specimens appears to be constant and implies that paired members of *P. variabilis* were not symmetrical. Other examples of this asymmetry are to be seen in the genera *Cavusgnathus*, *Scaphignathus*, *Mestognathus* and *Pseudopolygnathus*.

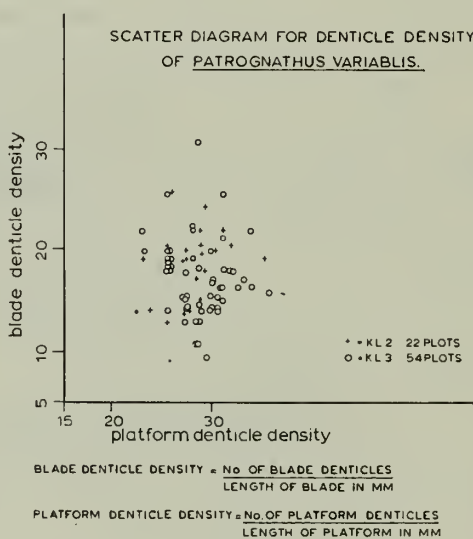


FIG. 35. Scatter diagram to show the relationship between the density of denticles on the blade and those on the platform of the species *Patrognathus variabilis*.

Genus *PLECTOSPATHODUS* Branson & Mehl 19331933 *Plectospathodus* Branson & Mehl : 47.TYPE SPECIES. *Plectospathodus flexuosus* Branson & Mehl.*Plectospathodus* ? sp. nov. A

Plate 25, figs. 8a-9

MATERIAL. 3 specimens : figured, X 312, X 313.

RANGE. North Crop ZLA 33.

DESCRIPTION. A plectospathodid characterized by a long anterior bar ; denticles free standing, sub-circular in cross-section and posteriorly inclined ; those in the median third the largest. Apical denticle larger than bar denticles, ovate in cross-section, and posteriorly and laterally inclined. Posterior bar about equal in length to anterior bar, twisted and with slight inward curvature, the posterior tip down-flexed. Denticles small, fine, except for terminal denticle, which is as large as apical denticle, and may have small denticles developed on its posterior face.

The basal cavity is open, flared on the inner side, with a " nick " in the inner lip beneath the apical denticle ; it extends beneath the posterior and anterior bars for a short distance.

REMARKS. The genus *Plectospathodus* has previously been described only from rocks of Upper Silurian and Lower Devonian age, but these specimens agree perfectly with the generic description given by Branson & Mehl (1933A : 47).

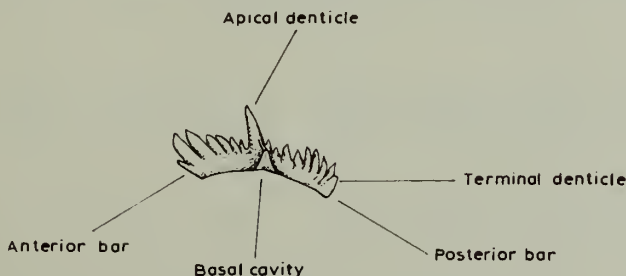
Plectospathodus ? sp. nov. B

Plate 25, figs. 10-12

MATERIAL. 4 specimens : figured, X 427, X 428, X 314.

RANGE. North Crop 3D 14/15-3D 19.

DESCRIPTION. Very small units consisting of two bars, roundly arched at their junction. Oral edges denticulate. A conspicuous apical denticle. Denticles of

FIG. 36. *Plectospathodus* sp. showing morphological terms used in the text.

variable size, inclined posteriorly ; at or near posterior end of unit a relatively enormous, greatly elongated denticle, slightly greater in basal width than apical denticle.

The inner lateral face is generally convex, with a rather flat oral shoulder on which the denticles are developed. The denticulation of the anterior bar consists of a series of rather small inconspicuous basally confluent denticles, all inclined equally posteriorly at an angle of about 45° to the oral edge of the bar. The anterior end is roundly spatulate and there is a very feeble basal flare below the apical denticle. The apical denticle is biconvex in cross-section, with blunt anterior and posterior edges, and is curved slightly inward, as well as being inclined posteriorly. On the posterior bar there is a series of denticles which decrease in size towards the distal end ; they are basally confluent and have sharp free tips, the most posterior, or the one next to it, being much the largest. The posterior portion of the posterior bar is straight-edged, but the posterior aboral corner is bluntly rounded. The whole aboral surface of the unit is gently concave in lateral view and the unit tends to be bowed inwards, as well as the main denticles being rather incurved. In outer lateral view the whole unit is rather flat and is slightly indented below the apical denticle. The basal surface is flared on the inner lateral face below the apical denticle, and there is a broad cavity in this position, which rapidly decreases anteriorly and posteriorly, to be extended along part of both bars as a shallow longitudinal slit.

Genus *POLYGNATHUS* Hinde 1879

1879 *Polygnathus* Hinde : 359.

TYPE SPECIES. *Polygnathus dubia* Hinde 1879.

Polygnathus communis communis Branson & Mehl

Plate 12, figs. 2a-5c

- 1934 *Polygnathus communis* Branson & Mehl : 293, Pl. 24, figs. 1-4.
 1934 *Polygnathus communis* Branson & Mehl ; E. R. Branson : 308, Pl. 25, figs. 5, 6.
 1938 *Polygnathus communis* Branson & Mehl ; Branson & Mehl : 145, Pl. 34, figs. 39-41.
 1939 *Polygnathus communis* Branson & Mehl ; Cooper : 399, Pl. 39, figs. 1, 2, 9, 10, 23, 24.
 1939 *Polygnathus adola* Cooper : 399, Pl. 39, figs. 33-36.
 1939 *Polygnathus marginata* Branson & Mehl ; Cooper : 401, Pl. 41, figs. 15, 16.
 1944 *Polygnathus communis* Branson & Mehl ; Branson & Mehl in Shimer & Schrock : 245, Pl. 94, figs. 29-31.
 1944 *Polygnathus communis* Branson & Mehl ; E. B. Branson : 208, 221, Pl. 39, figs. 39-41.
 1947 *Polygnathus communis* Branson & Mehl ; Mehl & Thomas : 15, Pl. 1, fig. 36.
 1949 *Polygnathus communis* Branson & Mehl ; Youngquist & Patterson : 62, Pl. 15, figs. 7, 8.
 1949 *Polygnathus communis* Branson & Mehl ; Thomas : 411, Pl. 3, fig. 70.
 1951 *Polygnathus communis* Branson & Mehl ; Youngquist & Downs : 787, Pl. 111, figs. 4, 5, 19, 20.
 1951 *Polygnathus communis* Branson & Mehl ; Hass : 2538, 2539, Pl. 1, fig. 10.
 1956 *Polygnathus communis* Branson & Mehl ; Bichoff & Ziegler : 156, Pl. 12, figs. 1-3.
 1956 *Polygnathus communis* Branson & Mehl ; Hass : 24, 25, Pl. 2, figs. 3-5.

- 1957 *Polygnathus communis* Branson & Mehl ; Bischoff : 42, Pl. 2, figs. 23-27.
 1957 *Polygnathus communis* Branson & Mehl ; Ziegler in Flügel & Ziegler : 46, Pl. 2, fig. 15.
 1959 *Polygnathus communis* Branson & Mehl ; Hass : 390, Pl. 49, figs. 9-11, 13.
 1959 *Polygnathus communis* Branson & Mehl ; Helms : Pl. 3, fig. 11.
 1959 *Polygnathus communis* Branson & Mehl ; Voges : 288, Pl. 34, figs. 1-7.
 1960 *Polygnathus communis* Branson & Mehl ; Ziegler : Pl. 1, fig. 9.
 1960 *Polygnathus communis* Branson & Mehl ; Dvorak & Freyer : 884-888, Pl. 1, figs. 15, 16.
 1960 *Polygnathus decorosa* Stauffer ; Dvorak & Freyer : 882, Pl. 2, figs. 1-2.
 1961 *Polygnathus communis* Branson & Mehl ; Beach : 49, Pl. 6, figs. 1-4.
 1961 *Polygnathus communis* Branson & Mehl ; Scott & Collinson : 130, Pl. 1, figs. 6-10 Pl. 2, fig. 30.
 1961 *Polygnathus communis* Branson & Mehl ; Freyer : 70.
 1962 *Polygnathus pura* Voges ; Müller : 1388, text-fig. 2a, b.
 1964 *Polygnathus communis communis* Branson & Mehl ; Rexroad & Scott : 33, Pl. 2, figs. 17, 18.
 1964 *Polygnathus communis* Branson & Mehl ; Higgins, Wagner-Gentis & Wagner : 225, Pl. 5, fig. 30.
 1964 *Polygnathus communis* Branson & Mehl ; Budurov & Tschurner : Pl. V, figs. 1a, b, 2a, b, 12, 18.
 1965 *Polygnathus communis* Branson & Mehl ; Spasov : 95, Pl. 2, figs. 15, 15a.
 1965? *Polygnathus communis* Ethington : 581, Pl. 67, fig. 7.

MATERIAL. 740 specimens : figured, X 346, X 347, X 348.

RANGE. North Crop KL 3-ZL 10, Avon Gorge K 3-C 9.

DESCRIPTION. The platform varies in shape from ovate to lanceolate, but is unornamented except for a medial nodose carina. The platform edges tend to be upturned and thickened. The anterior blade varies in length but is commonly equal to the platform length, bearing from 10 to 16 laterally compressed, fused denticles ; the oral outline of the blade is convex.

In aboral view the cavity is fairly large, circular, and situated at the junction of the platform and the anterior blade. In some specimens the cavity appears on the blade. The aboral surface of the unit posterior to the cavity tends to be concave. The cavity is extended as a tapering slit along the anterior blade, to a point just anterior to its mid point. A keel runs from the margin of the main cavity to the posterior tip of the platform ; its aboral surface may bear a fine groove. The aboral surface makes a sharp obtuse angle with the lateral faces of the outer platform margins, giving a chine-like aboral appearance to the unit.

REMARKS. Carinate and bifurcate subspecies of *Polygnathus communis* known from America are not present in our fauna, but the species is very variable throughout the section. A single specimen (Pl. 12, 1a-c) is obviously close to individual specimens assigned to this species, but differs in the general form of the oral surface of the platform. The anterior lateral margins of the platform are strongly constricted and upturned, giving almost a *Siphonodella*-like appearance to the anterior portion. The posterior portion is wide, shallow and bluntly rounded posteriorly, the whole having the general appearance of a shallow spoon. There is no ornamentation and the carina continues as a series of distinct blunted nodes to the posterior end of the

platform, the most posterior node being the smallest of the six exposed on the broken specimen.

Polygnathus bischoffi sp. nov.

Plate 13, figs. 8a-IIC

1957 *Polygnathus inornata* E. R. Branson ; Bischoff : 42, Pl. 2, figs. 17, 18, 20, 21.

1959 *Polygnathus* cf. *flabella* Branson & Mehl ; Voges (*partim*) : Pl. 34, fig. 11 only.

1964 *Polygnathus inornata* E. R. Branson ; Higgins : 225, fig. 4, Pl. V, fig. 29.

DERIVATION OF NAME. After Dr. G. Bischoff.

DIAGNOSIS. Arrow-shaped platform ; widest in anterior half, tapering to pointed posterior. Unit usually slightly arched in lateral view. Platform ornamented by delicate ribs, confined to margin. Platform margin upturned in anterior half. Small basal cavity, circular in outline, with thickened lips, situated anteriorly.

MATERIAL. 64 specimens : Holotype X 349, Paratypes X 350, X 351, Hypotype X 352 (all figured).

TYPE LOCALITY AND HORIZON. South Wales Coalfield. Sample SCC, C Zone, Fall Bay, Gower.

RANGE. Avon Gorge C 11-C 24.

DESCRIPTION. The platform is arrow-shaped, with a straight to slightly curved axis. In lateral view the unit is arched. The platform is widest anteriorly, and at

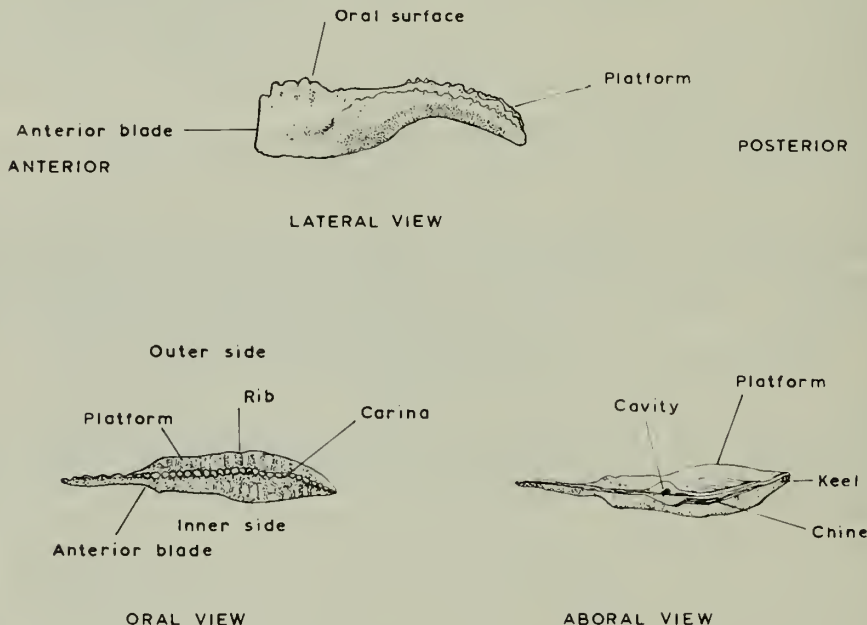


FIG. 37. *Polygnathus* sp. showing morphological terms used in the text.

mid-length it is only slightly narrower than at the anterior. The platform is two and a half times as long as wide and tapers to the pointed posterior. The margins of the platform are slightly upturned in the anterior and mid-thirds, and the oral surface is ornamented by a number of transverse ridges, which are more strongly developed at the margin. The margins of the platform are equal in height to the carina and on either side of the carina there is a trough, which is more strongly developed at the anterior. The trough opens to the anterior. The anterior blade is of the same length as the platform and consists of 6 denticles, which are highest at mid-length. The carina consists of nodes fused for their entire length and extends a short distance beyond the posterior extremity of the platform. The basal cavity; situated in the anterior third of the aboral surface, is small and rounded in outline, with thick lips. In some specimens a groove extends posteriorly from the basal cavity to the posterior extremity of the unit.

REMARKS. Compared with *Polygnathus inornatus inornatus* the platform of *P. bischoffi* is more elongate, broader in the anterior half and tapering uniformly in the posterior half. The platform also has more convex margins and is arched in lateral view. *Polygnathus bischoffi* has less strongly developed anterior troughs than *Polygnathus inornatus inornatus*, because the margins of the platform in the anterior third are not as strongly upturned.

Polygnathus bischoffi is characteristic of the C Zone both in the Bristol area and in other parts of the South West Province. It makes its first appearance near the base of the *Laminosa* Dolomites. Bischoff obtained the specimens of *Polygnathus inornatus* which he illustrated from the Cu II *Siphonodella* Subzone. A specimen, which Voges referred to as *Polygnathus* cf. *flabellus*, and which is here placed in synonymy, was found by him in the *Siphonodella p. triangulus triangulus* Zone, which is Upper Cu I in age.

The "*Polygnathus inornata*" group

Rexroad & Scott (1964 : 35) remarked that "*P. inornata* is a remarkably varied species". They included within their concept of this species *P. sagittarius* Youngquist & Patterson, a junior synonym of *P. lacinatus* Huddle which we regard as a separate and variable species in its own right. However, even within the much narrower terms of our present diagnosis, there is still a marked degree of variability.

The transition between *P. inornatus* and *P. lobatus* was noted by Rexroad & Scott (1964 : 35), and can also be seen in our faunas. There is also a tendency for the development of a rostral ridge in both *P. inornatus* and *P. lobatus*. In a few cases, breakdown of the transverse platform ridges into transverse lines of nodes is also seen. The *P. inornatus* fauna occurs within the range of the genus *Siphonodella* and these morphological details are characteristic of that genus, which is extremely rare (0.5% of total conodont fauna) in our faunas. It seems that the *P. inornatus* group show morphological developments which carry it towards, but not as far as, the characteristic morphology of the genus *Siphonodella*.

The *P. inornatus* s.s. forms with a well-developed rostral ridge are here given sub-

specific rank as *P. inornatus rostratus* and the *P. lobatus* forms with the same feature are referred to *P. lobatus inflexus*.

***Polygnathus inornatus inornatus* Branson & Mehl**

Plate 10, figs. 4a-6c

- 1934 *Polygnathus inornata* Branson & Mehl : 293, Pl. 24, figs. 5-7.
 1934 *Polygnathus inornata* Branson & Mehl ; E. R. Branson : 309, Pl. 25, figs. 8, 26.
 1938 *Polygnathus inornata* Branson & Mehl ; Branson & Mehl : 132, 146, Pl. 34, fig. 37.
 non 1939 *Polygnathus inornata* Branson & Mehl ; Cooper : 400, Pl. 39, figs. 11, 12 (= *Polygnathus inornata rostrata*).
 1944 *Polygnathus inornata* Branson & Mehl ; E. B. Branson : Pl. 39, fig. 37.
 1949 *Polygnathus inornata* Branson & Mehl ; Youngquist & Patterson : 64, Pl. 17, figs. 4, 5, 9, 13.
 1949 *Polygnathus inornata* Branson & Mehl ; Thomas : 409, 411, Pl. 3, fig. 36.
 1951 *Polygnathus inornata* Branson & Mehl ; Youngquist & Downs : 787, 788, Pl. 111, figs. 17, 18 (non Pl. 111, fig. 11 = *P. lobata lobata*).
 non 1956 *Polygnathus inornata* Branson & Mehl ; Bischoff & Ziegler : 157, Pl. 12, figs. 4, 5 (= *P. flabella*).
 1956 *Polygnathus inornata* Branson & Mehl ; Hass : 25, Pl. 2, figs. 14, 15.
 non 1957 *Polygnathus inornata* Branson & Mehl ; Bischoff : 42, Pl. 2, figs. 17, 18, 20, 21 (= *P. lacinata lacinata*).
 non 1957 *Polygnathus inornata* Branson & Mehl ; Ziegler in Flügel & Ziegler : 46, Pl. 2, fig. 7 (= *P. nodomarginata*).
 1957 *Polygnathus inornata* Branson & Mehl ; Cloud, Barnes & Hass : Pl. 5, fig. 6.
 non 1958 *Polygnathus inornata* Branson & Mehl ; Klapper : 1089, Pl. 142, figs. 2, 3.
 1959 *Polygnathus inornata* Branson & Mehl ; Voges : 291, Pl. 34, figs. 12-16, (non Pl. 34, figs. 17-20 = *P. lacinata lacinata*).
 non 1964 *Polygnathus inornata* Branson & Mehl ; Higgins, Wagner-Gentis & Wagner : 225, Pl. 5, fig. 29 (= *P. lacinata lacinata*).
 1964 *Polygnathus inornata* Branson & Mehl ; Rexroad & Scott 35, Pl. 2, figs. 19, 20.

MATERIAL. 82 specimens : figured, X 353, X 354, X 355.

RANGE. North Crop KL 16-KL 20.

DESCRIPTION. The platform is semi-circular in cross-section and is ornamented by transverse ribs, which terminate on the platform edge as low nodes. The ridges may break up into transverse rows of nodes. The platform is fairly flat at the posterior, but anteriorly it has deep troughs, separated by a nodose carina. The whole unit is nearly symmetrical.

The carina is a continuation of the free blade, and runs the whole length of the platform, terminating at the posterior end in a point. The blade is thin and highest in its mid-part, the aboral outline being straight.

Aborally the unit is keeled, the basal cavity occurring as a small pit at, or just posterior to, the junction of the anterior blade and the platform. The cavity edges tend to be thickened.

REMARKS. Our specimens agree closely with those of Rexroad & Scott (1964).

Polygnathus inornatus rostratus subsp. nov.

Plate 10, figs. 7a-9c

? 1939 *Polygnathus irregularis* Cooper : 400, Pl. 39, figs. 57, 58.1962 *Pseudopolygnathus* ? cf. *Pseudopolygnathus triangula* Voges ; Müller : 1388, text-figs. 9a-c.

DERIVATION OF NAME. From the development of a rostral ridge on the inner platform.

DIAGNOSIS. *P. inornatus* possessing rostral or pseudorostral ridge on inner platform.

MATERIAL. 28 specimens : Holotype X 530, Paratypes X 356, X 357 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample KL 4.

RANGE. North Crop KL 4-KL 16-KL 20, ZL 1, Avon Gorge K 12-K 14.

DESCRIPTION. Specimens of *P. inornatus rostratus* agree closely with specimens of *P. inornatus* s.s., apart from the configuration of the inner margin. There is a tendency for the anterior part of the inner margin to move towards the anterior blade, the posterior part then becoming lobate. The anterior inner margin tends to run towards the carina for a very short distance in more advanced forms.

In some cases there tends to be a thickening of the aboral portion of the platform wall, so that in oral view the platform edge does not form the inner edge of the unit.

REMARKS. This subspecies includes all specimens showing a breakdown in the smoothness of the inner edge. Thus in more advanced forms a pseudo-rostral ridge can be seen (e.g. Pl. 10, fig. 7b). In less advanced forms there may be thickening of the aboral edge and a breakdown of the curvature of the inner edge (e.g. Pl. 10, fig. 9b). The strength of development of the ridge bears some relationship to both ontogeny and to stratigraphic position. This involves an offset, tilt and deflection towards the carina of the inner lateral margin, the pseudo-rostral ridge having a sharp and well-defined outer face. The posterior portion of the ridge, which runs sub-parallel to the carina, is conspicuously higher than the adjacent inner margin, although the posterior termination is low and indistinct.

Polygnathus inornatus vexatus subsp. nov.

Plate 10, figs. 1a-3c

DERIVATION OF NAME. From the troublesome problem of specific assignment.

DIAGNOSIS. Subspecies of *P. inornatus*. An arched unit with symmetrical platform, curved axis, and fairly long blade, composed of broad, fused, chevron-tipped denticles. Carina low, nodose, extending beyond platform as short posterior blade. Symmetrical lanceolate platform, ornamented with medium to strong transverse ribs ; platform edges serrated. Basal cavity small, occurring near junction of blade and platform.

MATERIAL. 5 specimens : Holotype X 358, Paratypes X 359, X 551 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample KL 19.

RANGE. North Crop KL 17-KL 19, Avon Gorge K 17.

REMARKS. As was noted by Rexroad & Scott (1964) *P. longiposticus* belongs to the *P. inornatus* group of polygnathids. It can be distinguished from *P. inornatus* s.s., by the lanceolate platform and the longer free blade. The present subspecies approaches *P. longiposticus* in these respects.

Polygnathus lacinatus Huddle

Certain polygnathids with a lanceolate platform and an elongate, excavated cavity were referred to a new species, *P. lacinatus*, by Huddle (1934). This species was recognized by Cooper (1939), but Youngquist with various co-authors (Youngquist & Patterson 1949, Youngquist, Miller & Downs 1950, and Youngquist & Downs 1951), referred similar forms to *P. sagittarius* Youngquist & Patterson. German workers, describing collections from condensed sequences of strata, included *P. lacinatus* within the species *P. inornatus* E. R. Branson, thus extending both the stratigraphic range and concept of that species. The distinctive feature of *P. lacinatus* is the marked longitudinal extension of the rim of the basal cavity, which is often half the total platform length (e.g. Pl. 11, fig. 9b).

P. lacinatus appears to us to be a valid species. It is restricted to an interval comparable with beds of Cu II β/γ age in Europe. Its generic affinities are somewhat doubtful. Huddle stated that the platform was a perfect polygnathid platform, although the basal cavity differs markedly from the "typical" cavity of that genus. The possession of a large basal cavity brings it within the morphological scope of the genus *Pseudopolygnathus*, but the lack of asymmetry of the cavity and the polygnathid nature of the platform lead us to conclude, like Huddle, that this form is a polygnathid. Later phylogenetic work may show that this is not the case. Within our faunas there appear to be several variants, and these have been referred to new subspecies. Forms referred to *P. lacinatus lobatus* show lobation of the posterior part of the outer platform, and considerable narrowing of the anterior part of the platform, with upturning of the platform edges. This tends to give these specimens an overall siphonodellid appearance, but the basal cavity and lack of rostral ridges set them apart from the genus *Siphonodella*.

Polygnathus lacinatus asymmetricus subsp. nov.

Plate 11, figs. 1a-4c

DERIVATION OF NAME. From the asymmetrical development of the platform.

DIAGNOSIS. Subspecies of *P. lacinatus* with reduced inner platform, giving asymmetrical platform outline.

MATERIAL. 295 specimens : Holotype X 361, Paratypes X 360, X 362, X 363 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample ZLA 32.

RANGE. North Crop ZLA 29–ZLA 33, Avon Gorge Z 33–C 20.

DESCRIPTION. The anterior blade and the anterior portion of the platform are exactly comparable with *P. lacinatus* s.s., but the posterior part of the inner platform is reduced and does not extend to the posterior termination, the carina being extended posteriorly as a short posterior free blade.

Polygnathus lacinatus circaperipherus subsp. nov.

Plate II, figs. 12a–15c

DERIVATION OF NAME. From the platform edge, which encircles the posterior portion of the platform.

DIAGNOSIS. *P. lacinatus* with platform margin complete around posterior part of platform; posterior section of carina obsolescent.

MATERIAL. 32 specimens: Holotype X 364, Paratypes X 365, X 366, X 367 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample ZLA 32.

RANGE. North Crop ZLA 17–ZLA 30, Avon Gorge C 7.

DESCRIPTION. This subspecies is very similar to *P. lacinatus* except for the posterior platform termination. The platform edge is wrapped around the posterior, the carina dying away before it reaches the posterior. In aboral view the keel is also terminated abruptly and the whole posterior of the unit is rounded off. The posterior outline may be expanded and club-like (e.g. Pl. 11, fig. 12b) to bluntly pointed (e.g. Pl. 11, fig. 15a). There is some variation in the form of the basal cavity. In some specimens it is extended relatively further posteriorly than in others. In neither case, however, is there an ungrooved posterior keel developed behind it.

REMARKS. This morphological variation is also seen in our faunas in the species of *P. communis*.

Polygnathus lacinatus lacinatus Huddle

Plate II, figs. 8a–10c

1934 *Polygnathus lacinata* Huddle: 95, Pl. 8, figs. 1–3.

1939 *Polygnathus lacinata* Huddle; Cooper: 401, Pl. 40, figs. 3, 4.

1949 *Polygnathus sagittaria* Youngquist & Patterson: 66, Pl. 15, figs. 9, 10.

1950 *Polygnathus* aff. *Polygnathus sagittaria* Youngquist & Patterson; Youngquist, Miller & Downs: 527, Pl. 67, figs. 2–4.

1951 *Polygnathus sagittaria* Youngquist & Patterson; Youngquist & Downs: 788, Pl. 111, figs. 7–9.

1959 *Polygnathus inornata* E. R. Branson; Voges: 291, Pl. 34, figs. 17–20 (non Pl. 34, figs. 12–16 = *P. inornata*).

MATERIAL. 753 specimens: figured, X 368, X 369, X 370.

RANGE. North Crop ZLA 29–ZL 19, Avon Gorge Z 32–C 20.

DESCRIPTION. The platform is lanceolate, from two to three times as long as wide, being widest at mid-point, narrowing considerably both to the anterior and to the posterior. The platform ornament consists of a fairly strong carina, often extended beyond the platform as a short posterior blade, the nodes being slightly higher in this region. There is an unornamented trough on either side of the carina, accentuated by the upturning of the platform edges, especially in the anterior. The upturned platform edges bear short transverse ridges, terminating in denticles, which give a crenulate platform edge. The ornament varies considerably; the juveniles tend to be smooth, and the strength of the ridges varies in the adults. The anterior blade is fairly long and high, consisting of 7 to 8 tall, laterally compressed, fused denticles, which are highest at the anterior end and decrease regularly in height towards the junction with the platform.

In aboral view the unit is very distinctive, the basal cavity being large and elongate. It tends to close slightly with age, but is always extremely large, being widest at the anterior, and narrowing gradually towards the posterior, where a short grooved keel is present.

REMARKS. This subspecies is distinguished by the large basal cavity. Forms described as *P. marginatus* Branson & Mehl, by Rexroad & Scott (1964 : 37) are recorded as having large basal cavities and may be referable to *P. lacinatus* s.s., but the lack of an aboral illustration makes us hesitate to include them in the present synonymy. Orally this subspecies is highly variable, and some forms might be mistaken for *P. inornatus*. The most distinctive feature is, however, the form of the basal cavity. In this, apart from the length of the basal cavity proper, the most conspicuous feature is the very strong lateral and longitudinal extension of the lips around the cavity. These extend posteriorly to the cavity, and become obsolescent only in the posterior quarter of the unit, although they narrow posteriorly towards that point from their maximum at the posterior termination of the cavity. There is no chine-like structure on the aboral surface, and the low-angle sloping outer aboral margins of the platform join the lateral lips of the cavity at a sharp angle. Most specimens tend to show an almost siphonodellid development of the anterior end of the platform, though this itself shows some variation. The *Siphonodella*-like spout of *P. lacinatus prelobatus* is even more strongly developed than that of the present subspecies. The strongly developed posterior aboral extension of the carina, and the deep anterior blade give a distinctive appearance to the platform in lateral view. It tends to "ride high" on the surface of the lateral blade.

Polygnathus lacinatus prelobatus subsp. nov.

Plate 11, figs. 5a-7b, 11a-c

DERIVATION OF NAME. From the lobate nature of the inner platform.

DIAGNOSIS. Subspecies of *P. lacinatus* with lobate postero-inner platform.

MATERIAL. 179 specimens : Holotype X 371, Paratypes X 372, X 373, X 374 (all figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample ZLA 32.

RANGE. North Crop ZLA 29-ZLA 33, Avon Gorge Z 33-C 9.

DESCRIPTION. The free blade and outer platform are closely similar to *P. lacinatus* s.s., but there is modification of the inner posterior platform margin. The postero-inner portion tends to be produced as a lobe, narrowing rapidly to the posterior termination, which is formed by a posterior projection of the carina, to give a short posterior anterior blade. The anterior inner platform tends to be considerably upturned and the platform edge is very close to the anterior blade. In aboral view the unit exhibits the characteristics of *P. lacinatus* s.s.

REMARKS. The narrowing of the anterior portion of the platform and the lobation of the posterior inner platform give this subspecies the aspect of *Siphonodella*, but the basal cavity precludes the inclusion of these forms in this genus.

Polygnathus lobatus lobatus Branson & Mehl

Plate 9, figs. 5a-8c

- 1938 *Polygnathus lobata* Branson & Mehl : 146, Pl. 34, figs. 44-47.
 1939 *Polygnathus lobata* Branson & Mehl ; Cooper : 401, Pl. 39, figs. 29, 30.
 1939 *Polygnathus curta* Cooper (*partim*) : 400, Pl. 39, figs. 37, 38 only.
 1949 *Polygnathus lobata* Branson & Mehl ; Thomas : 411, 418, Pl. 3, fig. 11.
 1949 *Polygnathus cumulae* Youngquist & Patterson : 62, Pl. 15, figs. 11-15.
 1951 *Polygnathus inornata* Branson & Mehl ; Youngquist & Downs : 787, Pl. 111, fig. 11
 (non Pl. 111, figs. 17, 18 = *P. inornata inornata*).
 1957 *Polygnathus lobata* Branson & Mehl ; Bischoff : 42, Pl. 2, fig. 19.
 1964 *Polygnathus lobata* Branson & Mehl ; Rexroad & Scott : 35, Pl. 2, figs. 15, 16.

MATERIAL. 21 specimens : figured, X 376, X 377, X 378, X 440.

RANGE. North Crop KL 16-KL 20.

DESCRIPTION. This unit is boat-shaped, with a curved axis. The platform is flat in the posterior portion but deepens to form two troughs either side of the carina in the anterior portion. The unit tends to be symmetrical in the anterior half, but in the posterior, the outer platform wall flares out to give a lobate process. The platform then narrows rapidly to give a pointed posterior termination. The ornament consists of transverse ridges dying out towards the carina and terminating on the platform edges as low nodes or short chevron-shaped denticles. The carina is sinuous, consisting of low nodes which merge with the free blade, which is itself short and high, being highest at its mid point.

In aboral view the unit is keeled, there being a small cavity posterior to the junction of the free blade with the platform. The antero-lateral corners project as two "horns" in aboral view. The whole central part of the aboral surface tends to be more or less flat and unornamented, except for the sinuous median ridge. The outer margin of this flattened chine-like area is sharp, and the flat sloping faces of the outer aboral edges join it at a sharp angle. The surface of the chine is finely striate, with the striations more or less parallel to the outer margins. In at least some specimens

(e.g. Pl. 9, fig. 6a-c, X 376), the aboral cavity is situated about a quarter of the total length of the platform from the anterior end.

REMARKS. This form is distinguished from *P. inornatus* s.s. by possessing a lobe on the outer margin. The two subspecies appear to be transitional.

***Polygnathus lobatus inflexus* subsp. nov.**

Plate 9, figs. 9a-c

DERIVATION OF NAME. From the inflexing of the inner platform margin.

DIAGNOSIS. *P. lobatus* in which inner anterior lateral margin is more or less strongly inflexed.

MATERIAL. 4 specimens : Holotype X 375 (figured).

TYPE LOCALITY AND HORIZON. North Crop. Sample KLM 1.

RANGE. North Crop KL 16-KL 20, Avon Gorge K 12.

DESCRIPTION. In a few specimens whose general characteristics are similar to *P. lobatus lobatus*, there is a marked tendency for the inflexing and upraising of the inner anterior lateral margin of the platform. This tends to be confined to the anterior third or half of the platform. The oral edge bears a series of irregular, low, rounded, confluent denticles, giving a bluntly serrate margin. It stands conspicuously higher than the carina and rather higher than the opposing outer lateral margin. It reaches almost the height of the large denticles in the median portion of the anterior blade, and it runs broadly sub-parallel to the line of the anterior portion of the carina. It is at the posterior end of this inflexed portion that the carina tends to be more or less strongly laterally deflected.

REMARKS. This form appears to be undergoing similar adaptations to those of *P. inornatus rostratus* within the species *P. inornatus*. This may imply either close relationships between *P. lobatus* and *P. inornatus* or independent (functional?) convergence.

***Polygnathus* sp.**

Plate 15, figs. 9a-c

MATERIAL. 1 specimen : figured, X 531.

RANGE. Farlow Sample FAR 4A.

DESCRIPTION. This specimen seems to be a pathological individual of the genus *Polygnathus*. It is distinguished by a lip-like secondary development on the inner lateral platform, so that although the anterior edge of the platform forms a typical, open, spout-like development on the inner lateral side and the inner anterior lateral margin, it is strongly developed and upturned. It ceases after running for about a quarter of the total length of the platform, and the platform itself is then bent outwards, as though some injury had taken place to the individual and then been reformed. The rather low sinuous margin of the platform gives a wide platform for

the middle half, but the whole platform is sharply tapered and is pointed posteriorly. There is a conspicuous lack of general ornament, except for barely perceptible transverse ridges and nodes on the outer lateral faces, and a median carina, which is also very inconspicuous, consisting of low fused nodes, which runs posteriorly from the anterior blade but does not divide the platform into two equal halves. It runs into the posterior portion of the platform. The anterior inner edge is higher than any other part of the platform except the median outer lateral edge, and is ornamented by low fused nodes, up to six in number.

In inner lateral view the "injury" to the inner lateral platform makes a prominent feature. The platform is deepest anteriorly and the "injury" shows a secondary projection.

In aboral view the individual shows a typical polygnathid form, with a minute and thickly-lipped cavity restricted to the anterior fifth of the platform, and extended anteriorly and posteriorly as a slit-like groove. The anterior blade is poorly preserved but it is relatively short, with a rounded anterior aboral margin, and has at least one conspicuous denticle near its posterior end.

Polygnathus sp.

Plate 31, fig. 21

MATERIAL. 3 specimens : figured, X 130.

RANGE. Avon Gorge D 22.

DESCRIPTION. Rexroad (1957 : 41) has noted the presence of small numbers of polygnathids in the Renault Formation at two localities. He has described three fragments, and very small numbers of specimens are also present in the D Zone of the Avon Gorge and the North Crop. In all three cases this represents an abnormally high stratigraphic occurrence of the genus. In the Mississippi Valley, for example, its generally accepted range extends upwards only into the Burlington Formation. A single specimen is illustrated. The anterior blade is broken, but this specimen displays strongly developed aboral lips with a conspicuous pit developed near the anterior end of the platform, and a well-developed slit-like basal cavity extending the whole length of the platform.

Genus *PRIONIODINA* Ulrich & Bassler 1926

1925 *Prioniodina* Bassler : 219 (*nom. nud.*).

1926 *Prioniodina* Ulrich & Bassler : 17, 18.

1934 *Subbryantodus* Branson & Mehl : 285.

TYPE SPECIES. *Prioniodina subcurvata* Ulrich & Bassler 1926.

In 1925 Bassler erected the generic name *Prioniodina*, and in 1926 with Ulrich as senior author, he gave the following description : "Base of tooth more or less curved, crowned with numerous, sub-parallel, rounded, discrete denticles all inclined in one direction, one of which located in the median third, is considerably larger than the others."

Later, Branson & Mehl (1934A) erected the genus *Subbryantodus* for "arched denticulate bars . . . with one or both limbs laterally flexed . . . denticles . . . laterally compressed . . . closely crowded . . . one denticle of exceptional size, the apical denticle at the apex of the arch . . . the aboral edge of the bar excavated beneath the arch apex by a long pit that tends to extend as a distinct groove along the edge of each limb".

Branson & Mehl suggested (p. 285) that *Subbryantodus* differed essentially from *Prioniodina* in the fused, laterally compressed denticles and tendency toward a split aboral edge. We consider that these differences are not of generic significance and regard *Subbryantodus* as a junior subjective synonym of *Prioniodina* Bassler 1925.

Prioniodina eireica (Collinson & Druce)

Plate 28, fig. 13

Subbryantodus eireica Collinson & Druce (in press).

MATERIAL. 1 specimen : figured, X 315.

RANGE. North Crop 3D 17.

DESCRIPTION. The distinctive features of this species are the minutely denticulated and very short depressed anterior bar, the massive, recurved, wide, pointed apical denticle, and the short straight feebly denticulated posterior bar. Below the

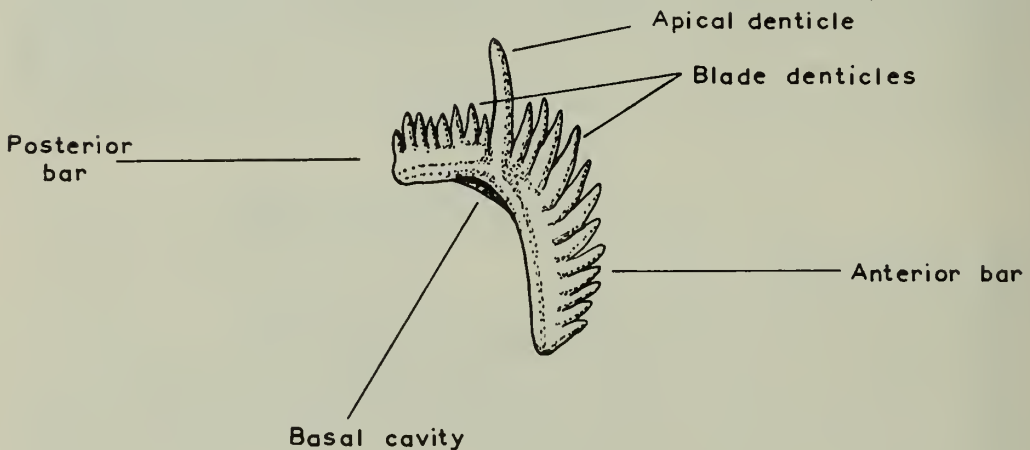


FIG. 38. *Prioniodina* sp. showing morphological terms used in the text.

posterior edge of the apical denticle there is a strongly flared basal cavity which, although laterally wide, is not very deep.

The whole unit is rather small and short and the apical denticle looks altogether too large for the general proportions of the anterior and posterior bars. The anterior bar is short, strongly recurved and slender in general construction, making an angle of about 130° with the straight basal margin of the posterior bar in outer lateral view. The anterior bar bears 2 or 3 small denticles with blunt free tips, but otherwise basally confluent. They have a tendency to increase in size posteriorly and stand more or less erect, or only gently posteriorly inclined, to the anterior bar. The anterior bar is of more or less uniform depth throughout its length, though it may be a little shallower anteriorly.

The apical denticle is strongly recurved on its anterior edge, but its posterior edge is straight or only feebly curved. It is sharply pointed and very broad at its base, being about five or six times as wide as the largest adjacent denticles. It has sharp anterior and posterior edges and gently convex lateral faces. The posterior bar is short and minutely denticulate, the denticles being so closely crowded that they are virtually confluent, except for their blunted tips. The bar decreases in depth posteriorly and is slightly longer, though shallower than, the anterior bar.

The other conspicuous feature of the unit in outer lateral view is the widely flaring basal cavity, which forms a conspicuous feature below the posterior half of the apical denticle. It is less conspicuous in inner lateral view and the whole unit is slightly bowed inward, having flatter faces.

In aboral view the basal cavity is seen to be asymmetrical, being more widely flared on the outer lateral face than it is on the inner. On the inner lateral face, although there is less curvature, the convexity continues towards the tip of the posterior bar. The whole posterior bar, as well as the posterior half of the apical denticle, is excavated by the cavity, which is deepest below the posterior edge of the apical denticle. It is continued anteriorly as a minute slit.

REMARKS. Collinson and Druce have discussed the relationship of this species to similar species of the genus *Ozarkodina*.

Prioniodina laevipostica (Rexroad & Collinson)

Plate 28, figs. 11-12b

1963 *Ozarkodina laevipostica* Rexroad & Collinson : 19, Pl. 1, figs. 1-6.

MATERIAL. 31 specimens : figured, X 316, X 317.

RANGE. North Crop ZLA 6-ZLA 12, CYD 6-CYD 7.

DESCRIPTION. This species closely approaches *P. eireica*, but differs from it in the relatively stronger development of the anterior and posterior bars, the less massive apical denticle, and the rather less conspicuous basal cavity. Rexroad & Collinson (1963) noted that their species had a posterior bar which was only partly denticulate, but both their illustrations and the present specimens show that, in at least some individuals, the posterior bar is denticulate for most or all of its length. The present

individuals bear up to five closely set, but apically discrete, more or less sharply pointed denticles, which decrease in size posteriorly and which are inclined at about 45° to the aboral surface of the posterior bar. The posterior bar is deep in its anterior portion but tapers rapidly towards its posterior end. Its aboral margin is more or less straight.

The apical denticle is two to three times the width of the largest adjacent denticles and is sharply to bluntly pointed. There is considerable variation in the form of the distal end of the apical denticle (see Rexroad & Collinson 1963). Although the cavity is similar in general form, it is rather shallower and somewhat less asymmetrical than that of *P. eivica*, and its anterior extension is also rather more conspicuous. The edges of both the cavity and the slits along the anterior and posterior bars are also prominent.

REMARKS. Our specimens from the D Zone closely resemble those of Rexroad & Collinson in overall morphology and in the aboral configuration, but they differ in denticulation, our specimens having fewer denticles on the anterior bar and more on the posterior bar. However, Rexroad & Collinson mention that some of their specimens fall within the limits of our specimens. The variable dentition is thus due to variation within the species.

Prioniodina latericrescens (Branson & Mehl)

Plate 24, fig. 19

1934 *Lonchodina latericrescens* Branson & Mehl : 212, Pl. 14, fig. 20.

MATERIAL. 12 specimens : figured, X 429.

RANGE. North Crop KL 1-ZLA 4.

DESCRIPTION. The unit is bowed and arched, being laterally compressed in juveniles, but the bars becoming circular in cross-section in adults. The posterior and anterior bars are of equal length, bearing about 4 isolated, sub-circular, posteriorly inclined denticles. In aboral view the pit is fairly large and occurs beneath the apical denticle.

Prioniodina oweni sp. nov.

Plate 28, figs. 5a-c

DERIVATION OF NAME. After Mr. T. R. Owen.

DIAGNOSIS. Prioniodinid with greatly expanded basal cavity and restricted posterior bar.

MATERIAL. 13 specimens : Holotype X 330 (figured).

TYPE LOCALITY AND HORIZON. R. Clydach, Nr. Gilwern, Lower Z Zone. Sample ZLA 5.

RANGE. North Crop ZLA 3–ZLA 27.

DESCRIPTION. The anterior bar is short, bearing about 5 discrete, sub-circular, posteriorly inclined denticles, whose height increases posteriorly, culminating in the apical denticle, which is the largest. The posterior bar is very restricted, commonly bearing 1 or 2 small, discrete, sub-circular, posteriorly inclined denticles.

In aboral view the whole unit is excavated, the basal cavity being expanded and pear-shaped at the posterior end. The widest part occurs beneath the apical denticle and it narrows gradually beneath the anterior bar, and rapidly beneath the posterior bar. The posterior termination tends to be rather blunt. The cavity lips in the posterior part are thickened to give a small flange.

REMARKS. The large basal cavity with excavated bars, together with the short posterior bar, precludes the placing of this species within the genus *Ozarkodina*, and serve to distinguish it from all other prioniodinids.

Prioniodina prelaevipostica sp. nov.

Plate 24, figs. 1–6

DERIVATION OF NAME. Ancestral form of *Prioniodina laevipostica* (Rexroad & Collinson).

DIAGNOSIS. Short *Prioniodina*, with large apical denticle and deflected anterior bar.

MATERIAL. 9 specimens : Holotype X 334, Paratypes X 333, X 331, X 332, X 335, X 336 (all figured).

TYPE LOCALITY AND HORIZON. R. Clydach, Nr. Gilwern, uppermost Z Zone. Sample ZLA 33.

RANGE. North Crop ZLA 32–ZL 19.

DESCRIPTION. The whole unit is arched, being surmounted by a tall, laterally compressed, free standing, posteriorly inclined apical denticle. The anterior bar is short, depressed through 45° and slightly deflected, bearing 2 or 3 tall isolated denticles, the most anterior ones being very small and posteriorly inclined.

The posterior bar is longer than the anterior, being fairly deep, shallowing posteriorly, and bearing 4 or 5 triangular denticles which are laterally compressed and posteriorly inclined.

In aboral view the unit is excavated beneath the apical denticle and the posterior bar, the cavity having flared lips. Beneath the anterior bar there is a narrowing groove.

REMARKS. This species is very similar to *P. laevipostica* (Rexroad & Collinson) which should be referred to the genus *Prioniodina*. The two species differ in the degree of curvature of the anterior bar, our species being much less curved, and in the dentition of the posterior bar, on which *P. laevipostica* bears 4 or 5 well-formed denticles. The obvious morphological similarities of these two species lead us to believe that *P. prelaevipostica* is the precursor of *P. laevipostica*.

Prioniodina stipans (Rexroad)

Plate 28, figs. 7a-10c

1957 *Subbryantodus stipans* Rexroad : 39, Pl. 4, fig. 1.1961 *Subbryantodus stipans* Rexroad ; Higgins : 219, text-fig. 6, Pl. 12, fig. 14.1962 *Subbryantodus stipans* Rexroad ; Higgins : 13, text-fig. 2, Pl. 1, fig. 9.

MATERIAL. 105 specimens : figured, X 337-X 340.

RANGE. North Crop 3D 10-3D 22.

DESCRIPTION. The most distinctive features of this species are the relatively short but strongly curved general form, with a series of subequal pointed denticles, the apical denticle being only slightly larger than those of its neighbours, and the wide flaring and greatly longitudinally extended basal cavity.

The basal cavity is greatly elongated and extends almost to the posterior end of the posterior bar, and about two-thirds the way to the end of the anterior bar. It is biconvex in outline, very deep, and slightly asymmetrical, with thin lateral edges. The anterior bar is about equal in length to the posterior, but is rather deeper, although it decreases slightly in depth anteriorly. The whole basal margin of the unit is deeply concave in inner lateral view and the anterior bar is conspicuously bowed inward. There is a rather inconspicuous shoulder developed about two-thirds of the height from the aboral margin to the base of the denticles. The anterior bar bears a series of about 12 denticles, confluent for most of their length, but bluntly pointed in their free apices. They have strongly convex lateral faces in their free portions and flat to gently convex lateral faces in their confluent portions, their free edges being more or less sharp. Those in the posterior two-thirds of the bar are of more or less uniform height and are regularly inclined posteriorly at about 45° to the bar, but those in the anterior third of the bar decrease in height towards the anterior end, and the most anterior two or three denticles are relatively inconspicuous and wholly confluent.

The apical denticle is about twice as wide as the adjacent denticles, and is about twice as long as adjacent denticles of the anterior and posterior bars. It is inclined at about 45° to the adjacent aboral surface.

The posterior bar is sharply recurved and bears a series of about 7 sharply pointed and partly fused denticles, which are strongly laterally compressed, and which tend to decrease in size posteriorly, especially in the posterior third.

Prioniodina subaequalis (Higgins)

Plate 28, figs. 1a-4

1961 *Subbryantodus subaequalis* Higgins : 218-219, Pl. 12, fig. 15, text-fig. 6.1963 *Subbryantodus subaequalis* Higgins ; Bouckaert & Higgins : 17, fig. 3.*Subbryantodus subaequalis* Higgins ; Collinson & Druce (in press).

MATERIAL. 143 specimens : figured, X 341-X 344.

RANGE. North Crop 3D 10-3D 22.

DESCRIPTION. The most striking features of this species are the confluent denticles of the long anterior bar, and the large denticles of the posterior bar. There is no conspicuous apical denticle, and the denticles of the posterior bar are discrete.

In aboral view the unit is straight in its median two-thirds, but both the anterior and the posterior ends are sharply flexed inwards. There is a deep and relatively conspicuous basal cavity below the apical denticle, and this is extended as a wide deep groove along the greater length of the anterior bar, and as a shorter narrowing groove below about half the length of the posterior bar. The edges of the cavity and of the aboral surfaces of the bars are relatively thin.

This is a somewhat variable species, but the anterior bar is generally rather longer and deeper than the posterior, and tends to be rather straight along its aboral margin when seen in inner lateral view. It bears a series of 9 or 10 laterally compressed denticles which are confluent at their bases and which are inclined posteriorly. In some specimens they show an alteration in size, and they also show a general tendency to increase in size posteriorly. Their free edges are sharp and their lateral faces are strongly convex, especially in the posterior half of the anterior bar. They show some variation, in that in some specimens they are free for the greater part of their length, but this is a relatively unusual feature.

There is no apical denticle in the strict sense, but the 2 or 3 denticles at the point of flexure of the unit tend to be larger than any of the other, and to be more or less equal in size. They are free for most of their length and they are inclined posteriorly, the degree of inclination increasing towards the posterior end of the series. They have sharp anterior and posterior edges and all taper sharply to their pointed tips. They have gently convex lateral faces. Behind them is a series of up to 5 discrete and strongly posteriorly inclined denticles, which in some specimens have smaller denticles separating them. There is a rather indistinct apical lip at the point of flexure. The posterior bar tends to decrease in depth posteriorly and its posterior aboral margin is gently curved.

Prioniodina ? sp. nov.

Plate 28, figs. 6a-c

MATERIAL. 1 specimen : figured, X 345.

RANGE. Scotland GILM 3.

DESCRIPTION. A single specimen is tentatively referred to the genus *Prioniodina*. It is characterized by an elongate straight anterior bar, which is continuous, without any vertical flexure with the straight, but broken, posterior bar. The anterior bar has convex lateral shoulders on the inner lateral face, and a straight inner lateral face below them. Its oral surface bears 5 discrete short denticles with sharply pointed tips, and posterior edges which are sharp ; they taper uniformly from their point of origin and stand more or less erect or only slightly inclined to the anterior bar. They show a slight tendency to increase in height posteriorly. The posterior bar bears at least 3 closely spaced, but discrete, sharply-pointed denticles. That nearest to the apical denticle is larger than the other two. They are strongly

laterally compressed, with sharp anterior and posterior edges and gently convex lateral faces. The apical denticle is about three times as wide as the adjacent denticles and two to three times as long. Its sharp anterior and posterior edges taper uniformly to a point and it is gently inclined to the posterior bar. Along the whole inner lateral length of the anterior and posterior bars there is a more or less conspicuously convex shoulder below the point of origin of the denticles. In outer lateral view the whole unit is somewhat flatter and the denticles are seen to curve slightly inwards. In aboral view the unit is excavated by a thin slit, which is very narrow anteriorly, but which increases regularly in width posteriorly, being widest posterior to the apical denticle, though there is no sign of lateral flare on the edges below the apical denticle.

Genus *PSEUDOPOLYGNATHUS* Branson & Mehl 1934

1934 *Pseudopolygnathus* Branson & Mehl : 297.

1939 *Macropolygnathus* Cooper : 392.

TYPE SPECIES. *Pseudopolygnathus prima* Branson & Mehl 1934.

THE ORIGIN AND NATURE OF THE GENUS

Pseudopolygnathus developed from *Spathognathodus* in the late Devonian and early Mississippian. *Spathognathodus anteposicornis*, *S. plumulus plumulus* sp. nov. and *S. aculeatus* have lateral denticles developed on one side of the blade and *S. costatus sulciferus* has lateral denticles on both sides of the blade. Branson and Mehl (1934A : 298) have reported a series of specimens which are transitional between *Spathognathodus* and *Pseudopolygnathus*. Voges (1959 : 296, fig. 4, & 297, fig. 5) has also illustrated a similar transitional series in the west German Cu I faunas.

Homoeomorphy among recurrent laterally nodose spathognathodids within the present fauna, is discussed below (p. 239). Thus, since the laterally nodose spathognathodids are homoeomorphic, and at least three chronologically distinct evolutionary lines have been demonstrated, it follows that the genus *Pseudopolygnathus* is polyphyletic.

This can be seen in our faunas. A Lower K Zone species is known, but there is then a complete absence of pseudopolygnathids until the Upper Z Zone is reached in the North Crop, and the Lower Z Zone in the Avon Gorge.

The Lower K Zone forms probably arose from the platform evolution of Upper Devonian to VI nodose spathognathodids. The Upper Z Zone forms, however, can be seen to have evolved directly from forms herein called *S. costatus sulciferus*, which are stratigraphically restricted to the lower and middle parts of the Z Zone.

HOMOEOMORPHY AND TAXONOMY

As in the spathognathodids, the existence of homoeomorphy in the pseudopolygnathids involves some problems in nomenclature. Since, however, most species of the genus were described by E. R. Branson (1934) from the Hannibal Formation of Missouri, in association with forms such as *S. costatus sulciferus*, it is probable that

our upper two forms are part of the same phylogeny and should be referred to Branson's species, whereas the homoeomorphic Lower K Zone forms are of distinct origin and are best regarded as new species.

AFFINITIES

Hass and others have considered that *Macropolygnathus* Cooper, 1939 is a junior subjective synonym of *Polygnathus* Hinde, 1879. The basal cavity of *Macropolygnathus ithus*, the type species of *Macropolygnathus*, is more akin to *Pseudopolygnathus* than to *Polygnathus*, and transitional forms have been found between *M. ithus* and *P. fusiformis*. We have, therefore, placed *Macropolygnathus* in synonymy with *Pseudopolygnathus*.

Pseudopolygnathus is distinguished from *Polygnathus* by its laterally expanded basal cavity.

ORIENTATION

In *Pseudopolygnathus primus*, the curvature of the longitudinal axis of the conodont and the shape of the basal cavity are bilaterally symmetrical elements. The ornamentation of the platform and a cross section through the blade, near the platform, are bilaterally asymmetrical elements.

The inner side of the conodont is concave and the outer side is convex. Forms are designated as right or left, when orientated with the blade placed in front and the convex side to the outside.

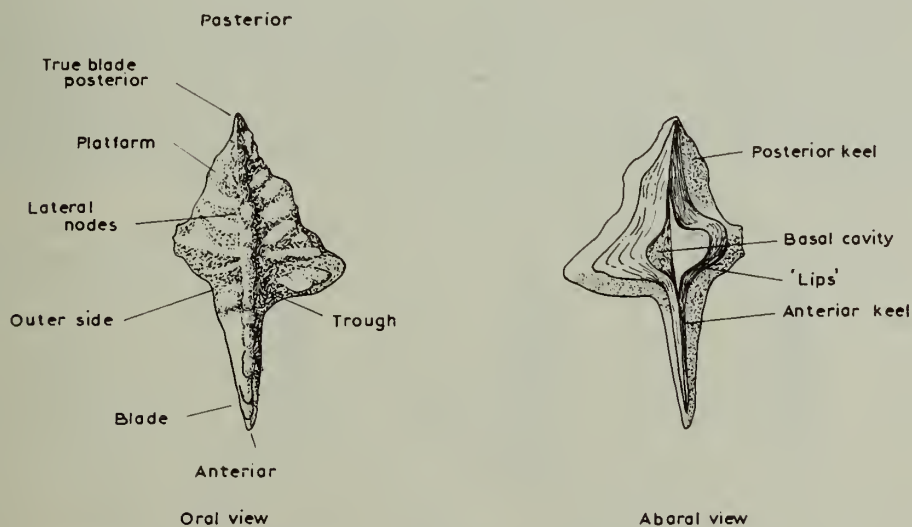


FIG. 39. *Pseudopolygnathus* sp. showing morphological terms used in the text.

THE EVOLUTIONARY DEVELOPMENT OF *PSEUDOPOLYGNATHUS*

There have been three distinct developments of the genus *Pseudopolygnathus* in the Avon Gorge : one in the lower and middle parts of the K Zone, referred to as the *Pseudopolygnathus vogesi* sp. nov. development, a second near the base of Z, the *Pseudopolygnathus primus* development and a third in the upper part of the Z Zone the *Pseudopolygnathus multistriatus* development.

The three developments have been along similar lines, the starting point of each being a straight, bladed spathognathodid with lateral denticles. Specimens of growth series from the three developments are, with the exception of adults, extremely difficult to distinguish (Fig. 43).

THE EVOLUTION OF *PSEUDOPOLYGNATHUS PRIMUS*

Voges (1959) noted that in the Upper Devonian the *Spathognathodus costatus* (*sensu* Bischoff & Ziegler) group marks the starting point in the evolutionary development of *Pseudopolygnathus primus*, and other pseudopolygnathids, which deviate from the typical bilateral symmetry of the spathognathodids. Voges recognized two groups within the *Spathognathodus costatus* group, right forms and left forms, the basal cavities of which are bilaterally symmetrical elements. The outer margin of the platform of right forms and the inner margin of left forms are both convex, and are thus bilaterally asymmetrical elements. In the left forms, there is a row of nodes or ridges on the inner side of the platform, which extends for three quarters the length of the unit. In the right forms, this row of nodes or ridges is on the outer side of the platform. In left forms, nodes are usually absent on the outer side of the platform, but in large specimens one or two nodes may be present on the outer side of the platform, situated near the basal cavity. Voges recognized two varieties of right forms, which correspond to the subspecies *Spathognathodus spinulicostatus spinulicostatus* (Bischoff 1957) and *S. spinulicostatus ultimus* (Bischoff 1957). In both these subspecies a secondary row of nodes or small ribs extends from the middle of the basal cavity to the posterior extremity on the inner side of the platform. In *Spathognathodus spinulicostatus ultimus* they are more strongly developed, and a furrow replaces the nodes along the posterior third of the blade.

Voges believed that *S. spinulicostatus spinulicostatus* and *S. spinulicostatus ultimus* were stages in the ontogenetic development of a right form, to which *Spathognathodus costatus* may be added as a left form. The opinion of Voges that *S. spinulicostatus ultimus* may represent an ontogenetic senile form of *S. spinulicostatus spinulicostatus* developed in the *Wocklumeria* Stage is not held by Ziegler (1962) who thinks it is unlikely that a fauna consisting entirely of senile members of *S. costatus (spinulicostatus) spinulicostatus* occurs at one horizon, while at a stratigraphically lower horizon, it consists entirely of non-senile members of *S. costatus (spinulicostatus) spinulicostatus*. In addition, Ziegler has found a few specimens of right forms of *S. costatus costatus* and a few left forms of *S. costatus (spinulicostatus) spinulicostatus* and *S. costatus (spinulicostatus) ultimus*.

Voges believed that from the first stage, represented by the *S. costatus* group, there

develops a second stage, represented by *Pseudopolygnathus dentilineatus* (see Voges 1959 : 297, fig. 5). In this second stage the outer margin of the platform of right forms and the inner margin of the platform of left forms are convex, and they are thus bilaterally asymmetrical elements. The outer part of the platform of left forms and the inner part of the platform of right forms consist of a few nodes, confined to the posterior part of the platforms. The basal cavities of right and left forms are bilaterally symmetrical elements. The two halves of the basal cavity are unlike in form, being characterized on the outside by a fold of the margin and a lip-like indentation of the edge. This form of the basal cavity is retained during further developments of the oral surface of the *Pseudopolygnathus primus* group.

Specimens of *P. dentilineatus* from the *P. dentilineatus* development of Voges, are very similar to specimens of *Pseudopolygnathus* from the lower and middle parts of the K Zone of the Avonian. These specimens are here referred to as *Pseudopolygnathus vogesi* sp. nov. and are typical of the Cu I stage of the Sauerland (Voges 1959). This is the lowest development of *Pseudopolygnathus* in the Avonian.

Voges was able to see the following further development of his Sauerland pseudopolygnathid faunas. The nodes and ridges of the outer part of the platform in left forms, and on the inner part of the platform in right forms, extend towards the anterior end and nearer the anterior extremity of the opposite side of the platform. In addition, a symmetrical element is present in the ornament of the platform, when the inner anterior angle of the platform becomes accentuated. *P. foliaceus* E. R. Branson, and *P. apetodus* Cooper are representatives of this stage.

The stage represented by *P. foliaceus* and *P. apetodus* develops into *P. triangulus inaequalis* and *P. triangulus triangulus*, which in the details of surface ornamentation, is a symmetrical element. In *P. triangulus*, the conspicuous asymmetry has disappeared and only the thickening of the blade near the platform on the right side, which is higher on the blade than the left, remains.

In the uppermost part of the K Zone of the Avonian, no specimens of *Pseudopolygnathus* have been found. There is a second development of *Pseudopolygnathus*—the *P. primus* development—near the base of the Z₁ Limestone. The specimens of this development are similar, but not identical, to specimens from the stage in Voges's development, which he described as including 'specimens similar to *Pseudopoly-*

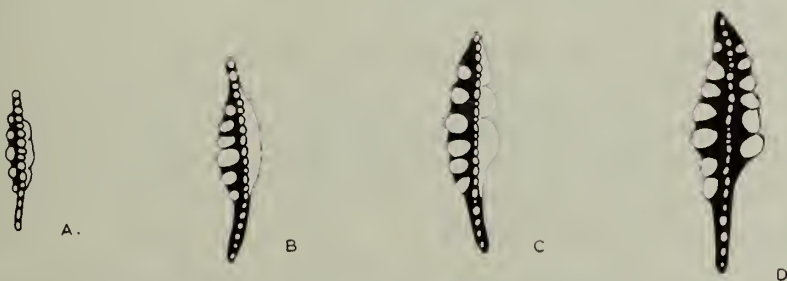


FIG. 40. Diagram to illustrate the ontogenetic development of pseudopolygnathids in the Z₁ Subzone of the Avonian.

gnathus foliaceus and *Pseudopolygnathus apertodus*'. They also closely resemble *P. primus* E. R. Branson, which occurs in the Chappel Limestone of Texas (Hass 1959).

The starting point for the *P. primus* development in the Avonian are specimens here referred to as *Spathognathodus costatus costatus*, which are found in the upper part of the K Zone and the base of the Z Zone. Forms with a row of lateral denticles, here referred to as *Spathognathodus costatus costatus* E. R. Branson, (they are not identical to *Spathognathodus bischoffi* sp. nov., but are homoeomorphs of the latter species) develop a ridge on the outer side of the left forms and on the inner side of the right forms. The edge of the ridge becomes crenulate and, at a later stage, nodes develop at the posterior extremity. The next stage is marked by an increase in the number of nodes along the ridge towards the anterior. The anterior extremity, on the outer side of the left forms and on the inner side of the right forms, extends as far anteriorly, as it does on the inner side of left forms and on the outer side of right forms. A small trough is present between the carina and the nodes of the ridge on the outer side of right forms and on the inner side of left forms. The nodes on the outer side of right forms, and on the inner side of left forms, become elongated to form ridges in later development, as also, in further development, do the anterior nodes of the outer side of left forms and on the inner side of right forms. Many bizarre forms can be formed as a result of the thickening of the ribs, but in most adults the trough at the anterior extremity of the outer side of left forms and on the inner side of right forms can still be detected.

A count was made of specimens of *Pseudopolygnathus* from a horizon 65 feet above

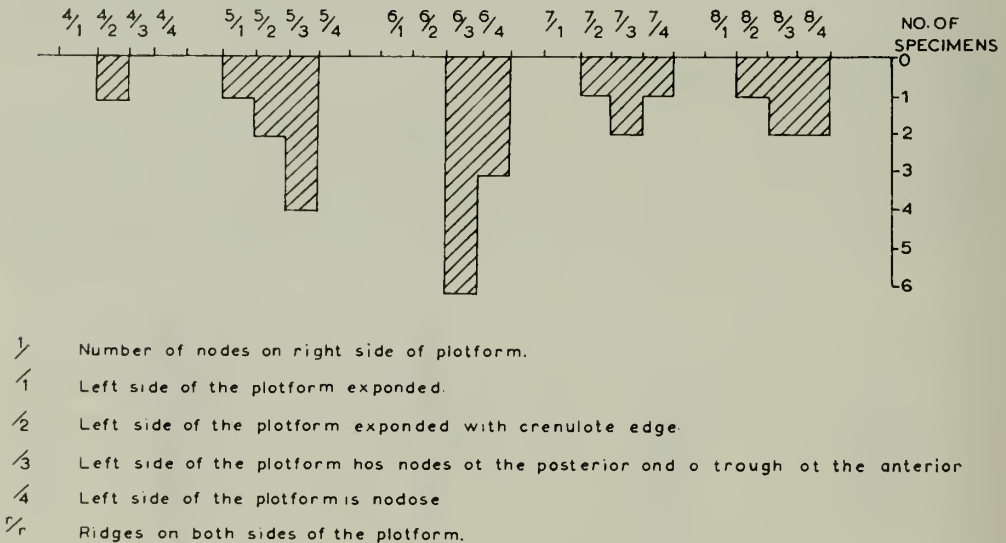
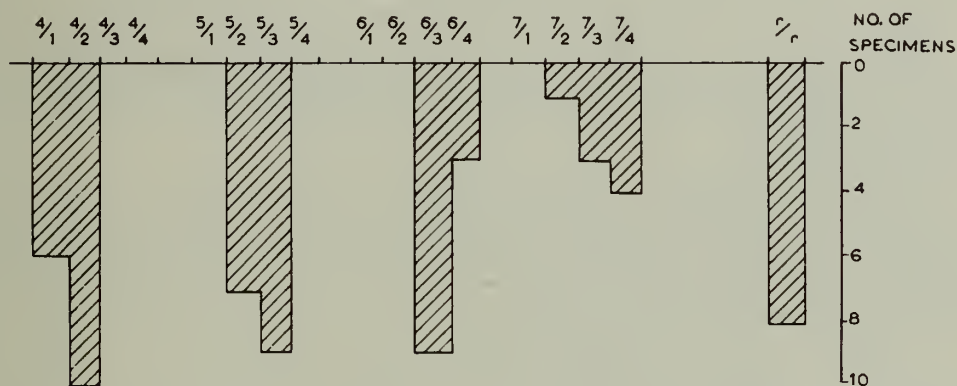


FIG. 41. Frequency diagram showing variation in the number of nodes and platform ridges in relation to platform shape in growth stages of a pseudopolygnathid population from a sample 65 ft. above the base of Z_1 in the Avon Gorge.

the base of the Z_1 Limestone in the Avon Gorge. The number of denticles on the right side of the platform was plotted, and also the character of the left side of the platform as marked by *a* a ridge, *b* a crenulated ridge, *c* a few denticles at the posterior and a trough at the anterior, or *d* nodes along its entire length. Adults were identified by the presence of ridges on both sides of the platform. The results showed that

- Forms with 4 nodes on the right side of the platform had either a ridge, or a crenulate ridge on the left side of the platform. No specimens were seen which had 4 nodes on the right side and nodes on the left side.
- Forms with 5 nodes on the right side of the platform had either a crenulate ridge, or a few denticles at the posterior end and a trough at the anterior end. No specimens were found with a straight edge to the ridge, or with denticles continuous on the left side.
- Forms with 6 denticles on the right side had either a few denticles at the posterior extremity of the left side and a trough at the anterior extremity, or they had a continuous row of denticles on the left side.

A similar plot was made of specimens higher in the section from Sample Z 21 at the base of Z_2 (fig. 25b). In this sample fewer specimens with 4 nodes on the right side of the platform were present (4%, as opposed to 25% in the lower horizon.)



- 1/ Number of nodes on the right side of the platform.
- 1 Left side of the platform expanded.
- 2 Left side of the platform expanded with a crenulate edge.
- 3 Left side of the platform has nodes at the posterior and a trough at the anterior.
- 4 Left side of the platform is nodose.
- 7/ Ridges on both sides of the platform.

FIG. 42. Frequency diagram showing variation in the number of nodes and platform ridges in relation to platform shape in growth stages of a pseudopolygnathid population from Sample Z 21 at the base of the Z_2 Subzone of the Avon Gorge.

This seems to indicate that the number of denticles on the right side of the platform is indicative of the ontogenetic age of the specimen and that the age is also reflected on the left side by the stage of development, through ridge, crenulated ridge, nodose posterior part of ridge and a continuously nodose ridge, culminating with the presence of ridges on both sides of the platform.

The stage of development in Voges's fauna represented by *Pseudopolygnathus triangulus inaequalis* and *Pseudopolygnathus triangulus triangulus*, which developed from the stage represented by *Pseudopolygnathus foliaceus* and *Pseudopolygnathus apetodus*, is not present in the Avonian. In the Avonian, specimens of *Pseudopolygnathus primus* are developed which consist of 7 ridges on the right side of the platform and a number of nodes confined to the outer margin on the left side of the platform, with a trough developed between the carina and the nodes of the left side of the platform. With further development, the nodes on the outer margin of the left side of the platform extend towards the carina to become ridges similar in outline to those on the right side of the platform. This development starts at first at the posterior end and extends towards the anterior, with the result that the platform on both sides of the carina consists of a number of ridges. The left side of the platform never extends as far to the anterior as the right side of the platform. In addition, a faint trace of a trough is present at the side of the carina, even in adult specimens. These forms are identical to *Pseudopolygnathus multistriatus* (Mehl and Thomas).

Higher in the section forms here referred to *Pseudopolygnathus* cf. *longiposticus* appear and they have the same outline as advanced species of *P. primus*; it is suggested, therefore, that they may represent a further stage in the development of *Pseudopolygnathus*.

The third development of *Pseudopolygnathus* in the Avonian—*P. multistriatus* development—takes place in Z₂. The specimen illustrated by Hass (1959, Pl. 47, fig. 21) as a juvenile of *Pseudopolygnathus lanceolatus* is a straight-bladed spathognathodid, with three lateral denticles. From such individuals the ontogenetic growth stages illustrated by Hass lead to the development of *P. multistriatus*.

In juveniles (which resemble *Spathognathodus tridentatus*) the denticles are developed on one side of the platform only; the opposite side develops at first by the formation of a slight ridge and, later, by the development of nodes on the ridge. A slight trough is again present on one side and this side is not developed as far to the anterior as is the other. Later development involves the replacement of nodes by ridges, which in adults become coarse and irregular.

Difficulty was experienced in the present study in separating juvenile specimens of *P. multistriatus* from adult specimens of *Pseudopolygnathus dentilineatus*. Specimens in the ontogenetic sequence of *P. multistriatus*, which are similar to *Pseudopolygnathus striatus* Mehl and Thomas, are identical to *P. dentilineatus* of Ziegler (1962). Bischoff (1957) and Voges (1959) include *P. striatus* in synonymy with *P. dentilineatus*. In view of the fauna associated with *P. striatus*, including *Gnathodus texanus* and *Gnathodus cuneiformis*, it seems likely that Rexroad and Scott's (1964) interpretation in placing *P. striatus* in synonymy with *P. multistriatus* is correct. This difference

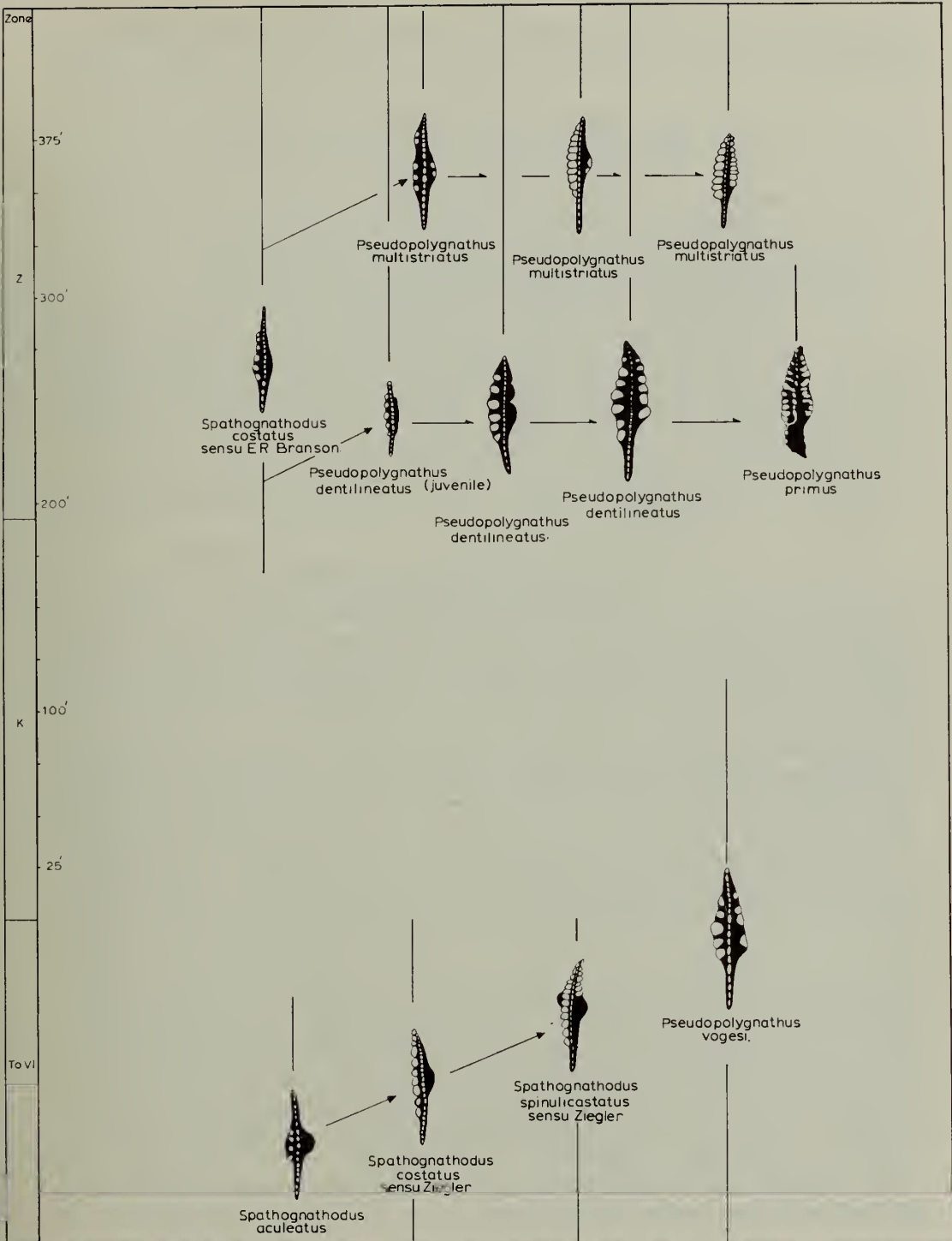


FIG. 43. Phylogeny of the genus *Pseudopolygnathus* and related forms in the Avonian. Vertical lines: stratigraphic range. Full arrows: phylogenetic development. Half arrows: morphological variation at one horizon.

in synonymy may explain the different stratigraphic ranges in North America and Germany for the two species in question.

Pseudopolygnathus dentilineatus E. R. Branson

Plate 5, figs. 9a-13c. Plate 6, figs. 8a-c

- 1934 *Pseudopolygnathus dentilineata* E. R. Branson : 317, Pl. 26, fig. 22.
 ?1934 *Pseudopolygnathus varicostata* E. R. Branson : 318, Pl. 26, figs. 19, 20.
 1934 *Pseudopolygnathus subrugosa* E. R. Branson : 318, Pl. 26, fig. 18.
 1934 *Pseudopolygnathus projecta* E. R. Branson : 320, Pl. 26, figs. 10, 11.
 1934 *Pseudopolygnathus brevimarginata* E. R. Branson : 319, Pl. 26, fig. 3.
 ?1939 *Pseudopolygnathus varicostata* E. R. Branson ; Cooper : 408-409, Pl. 40, figs. 44-45.
 ?1956 *Pseudopolygnathus striata* Mehl & Thomas ; Bischoff & Ziegler : 164, Pl. 11, fig. 20.
 non 1957 *Pseudopolygnathus dentilineata* E. R. Branson ; Bischoff : 50, 51, Pl. 4, figs. 30-32,
 (= *Pseudopolygnathus vogesi* sp. nov.) (Pl. 4, fig. 29 = *Pseudopolygnathus primus*)
 non 1959 *Pseudopolygnathus dentilineata* E. R. Branson ; Voges : 300-301, Pl. 34, figs. 49,
 50, text-fig. 5 II = *Pseudopolygnathus vogesi* sp. nov.
 non 1962 *Pseudopolygnathus dentilineata* E. R. Branson ; Ziegler : Pl. 2, figs. 10, 11.

MATERIAL. 182 specimens : figured, X 478, X 479, X 480, X 481, X 438, X 477.

RANGE. Avon Gorge Z 12-Z 28.

DESCRIPTION. This species is represented by pseudopolygnathids with an asymmetrical platform. Both the right and the left sides of the platform are ornamented with 4 to 7 nodes or ridges which are confined to the margin of the platform. The basal cavity is a symmetrical element, with a fold on the inner margin and a smooth convex outer margin in both right and left forms. The basal cavity, as pointed out by Klapper (1966 : 15), is as wide as the platform in aboral view.

This species has bilaterally asymmetrical right and left forms. The platform is two and a half times as long as wide, being widest at the anterior and narrowing to the pointed posterior. In adult specimens the platform is less triangular and more oval in outline. The margin of the right side of the platform in both right and left forms is convex and widest at mid-length : that of the left side of the platform is widest close to the anterior and narrows to the pointed posterior. The right side of the platform in both right and left forms extends further to the anterior than does the left side. The platform on either side of the carina is ornamented by 4 to 7 nodes or ridges, which are confined to the margin. There is usually one more node present on the right side of the platform than on the left. In smaller specimens a distinct trough may be present between the denticles of the margin and the carina, in the anterior half of the left side of the platform. A central straight to slightly curved nodose carina runs the length of the platform. The nodes of the anterior portion of the carina are stubby and wider than those of the posterior, which are more distinct and erect. The carina in smaller specimens extends a short distance beyond the posterior extremity of the platform.

The anterior blade, commonly composed of 6 denticles, is highest at the anterior end and slopes uniformly to the posterior.

In aboral view the basal cavity is large and occupies the anterior half of the platform ; the outer side of the margin has a slight fold. The basal cavities of right and left forms are bilaterally symmetrical elements.

REMARKS. In the basal beds of the Z Zone specimens of *P. primus* occur, which resemble *P. dentilineatus* in outline, but which differ in detail because the nodes or ridges of the right side of the platform are not confined to the margin, as in *P. dentilineatus*, but are elongated and extend into the carina. Also in adult *P. primus* there is a greater number of ridges than in adult *P. dentilineatus*. The anterior trough on the left side of the platform is present in both *P. dentilineatus* and *P. primus*, but in the latter species the nodes at the posterior of the left side of the platform are extended to the carina and form ridges. In addition the basal cavity is as wide as the platform in *P. dentilineatus*, but less wide in *P. primus*.

Higher in the section, forms resembling *P. dentilineatus* are found, but it is thought that they represent growth stages of other pseudopolygnathids. *P. striatus* Mehl and Thomas, for example, is similar to *P. dentilineatus* but can be shown by ontogenetic studies to be a growth stage of *P. multistriatus*.

We agree with Klapper (1966 : 15) that *P. dentilineatus* developed from double rowed forms of *Spathognathodus*. We do not regard *S. costatus ultimus* as their direct ancestor.

Pseudopolygnathus expansus sp. nov.

Plate 5, figs. 2a-c, 4a-c

DERIVATION OF NAME. After the expanded anterior part of the platform.

DIAGNOSIS. Pseudopolygnathid with straight axis in the mid and anterior thirds, but curved in the posterior third. Anterior third of the right platform is expanded. Outer margin, except expanded part, has convex outline and is ornamented by nine or more transverse ridges. Anterior to mid length of unit, margin of inner side of platform is expanded for a short distance. Basal cavity is asymmetrically flared ; both inner and outer anterior margins of basal cavity expanded laterally, but that of outer margin is greater.

MATERIAL. 3 specimens : Holotype X 483, Paratype X 482 (both figured).

TYPE LOCALITY AND HORIZON. Avon Gorge, the middle of the K Zone. Sample K 12.

RANGE. Avon Gorge, K 12.

DESCRIPTION. The platform is lanceolate in outline. The axis of the unit is straight in the mid and anterior thirds, but curved in the posterior third. The platform is widest anterior to mid-length and is two to three times as long as wide. The convex margin of the outer side of the platform is interrupted by a lateral expansion of the platform, mid-way between the anterior edge and the mid-length of the unit. The outline of the inner margin posterior to the mid-length is straight to slightly convex. At the mid-length the inner platform is expanded and tapers gradually from the expanded portion to the anterior extremity. The outer side of the platform is ornamented by up to nine transverse ridges, extending from the

margin to the carina. The inner side of the platform is ornamented by up to eleven ridges, the posterior two being nodose at the margin; the ridges in the posterior half of the inner platform extend to the carina from the margin. Those of the anterior half do not reach the carina and a trough is present, which is open to the anterior. The anterior edge of the inner part of the platform is lower on the carina than is the anterior edge of the outer part of the platform, which is at the same level as the carina. The 4 posterior denticles of the carina are nodose, but the remainder of the carina is composed of fused denticles.

The basal cavity is asymmetrical, pointed posteriorly and rounded anteriorly. Both the inner and outer margins of the basal cavity are expanded laterally in the anterior half. The anterior blade is of unknown form.

REMARKS. *Pseudopolygnathus expansus* sp. nov. is closely related to *Pseudopolygnathus vogesi* sp. nov. and transitional specimens have been found (Pl. 5, fig. 6-7), but is distinguished from it by the expanded anterior portion of the outer side of the platform. In this respect it resembles *P. primus* and is interpreted here as a homoeomorph of the latter species.

***Pseudopolygnathus* cf. *fusiformis* Branson & Mehl**

Plate 6, fig. 1

1934 *Pseudopolygnathus fusiformis* Branson & Mehl : 298, Pl. 23, figs. 1-3.

MATERIAL. 1 specimen : figured, X 552.

RANGE. Avon Gorge, C 14.

DESCRIPTION. A narrow platform is developed on either side of the strongly denticulate carina. The platform is widest anteriorly and tapers uniformly to the pointed posterior. In lateral view the platform is arched. The margins of the platform are notched and edged by 5 or 6 nodes. The blade is almost as long as the platform, and contains 7 denticles, which are fused with the high denticles of the carina. The carina is continued a short distance beyond the posterior extremity and bears 2 or 3 denticles. Aborally, there is a large basal cavity, typical of *Pseudopolygnathus*, which extends anteriorly to the junction of the blade and platform. It is rounded anteriorly and pointed posteriorly.

REMARKS. The specimen most closely resembles *Pseudopolygnathus fusiformis* Branson & Mehl, but it may be a juvenile of *Polygnathus*.

***Pseudopolygnathus* cf. *longiposticus* Branson & Mehl**

Plate 30, figs. 3, 7, 9-17

1934 *Polygnathus longipostica* Branson & Mehl : 294, 311, Pl. 24, figs. 8-11.

MATERIAL. 107 specimens : figured, X 522, X 523, X 433, X 434, X 545, X 442, X 443, X 448, X 449, X 547.

RANGE. Avon Gorge Z 11-C 7.

DESCRIPTION. The unit is straight, the platform being about twice as long as the blade. It is widest near mid-length and tapers to the posterior. The central carina is nodose and is continued a short distance beyond the posterior edge. One of the nodes of the carina near the posterior is higher than the others. The platform is ornamented by a number of short ridges near the outer margin, normal to the carina. The troughs between the carina and the ridges are unornamented. The anterior blade is high and composed of 5 fused denticles. In lateral view this species has a characteristic outline. The oral edge is highest at the anterior and slopes regularly to the posterior. The oral edge of the platform is arched convexly. The aboral edge is strongly concavely arched. In aboral view there is a very large pit and a strong keel.

REMARKS. The present specimens, although very close to *P. longiposticus*, differ in the outline of the platform, which more closely resembles that of *Polygnathus macrus* Cooper and *Polygnathus orthus* Cooper.

Pseudopolygnathus multistriatus Mehl & Thomas

Plate 5, figs. 14-16. Plate 6, fig. 2

- 1947 *Pseudopolygnathus multistriata* Mehl & Thomas : 16, Pl. 1, fig. 36.
 1947 *Pseudopolygnathus attenuata* Mehl & Thomas : 17, Pl. 1, fig. 9.
 1947 *Pseudopolygnathus rustica* Mehl & Thomas : 17, Pl. 1, fig. 8.
 1947 *Pseudopolygnathus striata* Mehl & Thomas : 17, Pl. 1, fig. 10.
 1957 *Pseudopolygnathus multistriata* Mehl & Thomas ; Bischoff : 51, Pl. 4, figs. 33, 35.
 1959 *Pseudopolygnathus lanceolata* Hass : 391, Pl. 47, figs. 16-26.
 1964 *Pseudopolygnathus multistriata* Mehl & Thomas ; Rexroad & Scott : 41, 42, Pl. 2, fig. 30.

MATERIAL. 46 specimens : figured, X 485, X 486, X 487, X 484.

RANGE. Avon Gorge Z 23-Z 29.

DESCRIPTION. This species is distinguished by the platform, which is not markedly asymmetrical ; it is ornamented by transverse ridges, usually nine or more on either side of the central carina. There is a short anterior blade, and a trough on the side of the carina in the anterior part of the left side of the platform. Adult specimens frequently have rough oral surfaces owing to the coarse nature of the ornament.

The platform is three and a half times as long as wide and has convex margins. The axis is straight to slightly curved and the platform on the left side of the carina does not extend as far to the anterior, as does the platform on the right side. The platform on either side of the carina is ornamented by 9 nodes which elongate into ridges reaching the carina. A slight trace of a trough is, however, present in the anterior part of the left side of the platform. The anterior two thirds of the carina is composed of fused denticles, but in the posterior third the denticles of the carina are free and distinct. The carina is continued a short distance beyond the posterior extremity of the platform. The anterior blade, composed usually of 5 denticles, is highest at the anterior and decreases in height to its junction with the carina. The

anterior blade is also equal in height to its length, and is curved in the opposite direction to the curvature of the posterior extension of the carina. The basal cavity, situated in the anterior part of the unit, is subcircular in outline, but more drawn out to the posterior than the anterior. It is as wide as the platform in juveniles, but in adults is less wide than the platform.

REMARKS. This species developed from *Pseudopolygnathus primus* by the extension of the nodes on the left side of the platform towards the anterior, and by a change in the platform ornament from marginal nodes to transverse ridges.

Pseudopolygnathus striatus, *P. rusticus*, *P. attenuatus* and *P. lanceolatus* are all considered to be growth stages of *P. multistriatus*. *P. striatus* is a homoeomorph of *P. dentilineatus*, as pointed out by Klapper (1966 : 15).

Lower Z forms referred to *P. dentilineatus* in this study (Pl. 6, fig. 8) resemble *P. multistriatus* (Pl. 5, fig. 16), but the left side of the platform is more strongly developed, and also there are 8 nodes or ridges on the right side of the platform in *P. multistriatus*.

The Avonian *P. multistriatus* pseudopolygnathids gave rise to *P. cf. longiposticus*.

Pseudopolygnathus nodomarginatus (E. R. Branson)

Plate 9, figs. 1a-4c. Plate 12, figs. 6a-8c, 10a-c

- 1934 *Polygnathus nodomarginata* E. R. Branson 310, Pl. 25, fig. 10.
 1934 *Pseudopolygnathus brevimarginata* E. R. Branson 322, Pl. 26, fig. 3.
 1934 *Pseudopolygnathus tenuis* E. R. Branson 319, Pl. 26, figs. 13, 14.
 1938 *Polygnathus flabella* Branson & Mehl : 147, Pl. 34, fig. 48.
 1939 *Polygnathus anida* Cooper : 399, Pl. 39, figs. 39, 40.
 1939 *Polygnathus flabellum* Branson & Mehl ; Cooper : 400, Pl. 39, figs. 13, 14.
 1944 *Polygnathus flabella* Branson & Mehl ; E. B. Branson : 208, 221, Pl. 39, fig. 48.
 1949 *Polygnathus anida* Cooper ; Thomas : 411, Pl. 3, figs. 10, 11.
 1950 *Streptognathodus* ? sp. Youngquist, Miller & Downs : 529, Pl. 67, figs. 12-14.
 1951 *Polygnathus* aff. *symmetrica* Branson & Mehl ; Youngquist & Downs : 789, Pl. 111, fig. 6.
 1956 *Polygnathus inornata* E. R. Branson ; Bischoff & Ziegler : 157, Pl. 12, figs. 4, 5.
 1957 *Polygnathus nodomarginata* E. R. Branson ; Bischoff & Ziegler : 157, Pl. 12, fig. 6.
 1959 *Polygnathus* cf. *flabellum* Branson & Mehl ; Voges : 290, Pl. 34, figs. 8-11.
 non 1959 *Polygnathus nodomarginata* E. R. Branson ; Helms : 251, Pl. 3, figs. 1a, b, c.
 1966 *Polygnathus nodomarginata* E. R. Branson ; Jones & Druce : 358, fig. 3, No. 3.

MATERIAL. 323 specimens : figured, X 488, X 489, X 490, X 491, X 492, X 493, X 494, X 495.

RANGE. North Crop ZLA 29-ZL 18.

DESCRIPTION. The platform is asymmetrical, one side being shorter than the other. In juveniles it is ornamented by a lateral row of nodes on each margin with a trough on either side of the medial carina (Pl. 9, fig. 1). With old age the rows of nodes expand into a platform with transverse ridges and the troughs tend to shallow (e.g. Pl. 12, fig. 6a). The carina is coarsely nodose and extends posteriorly, the juveniles often exhibiting a longer posterior free blade than the adults. The anterior blade is about half the platform length ; the highest denticles are developed anteriorly and

are just higher than the highest point of the platform in lateral view ; the blade is made up of 7 to 8 fused, laterally compressed, denticles.

In aboral view the basal cavity is lanceolate, being widest at the anterior end of the platform and narrowing gradually toward the posterior, where it becomes a narrow groove in a deep keel.

REMARKS. It appears that this species is closely related to *P. lacinatus*, the platform ornament serving to distinguish them.

The most distinctive features of the present species are its more or less laterally expanded basal cavity, its relatively strong ornament, and its relatively long blade. The platform ranges from elongate pointed to broadly lanceolate in oral outline.

It is difficult to decide whether this species is better assigned to the genus *Pseudopolygnathus* or to the genus *Polygnathus*, but because some specimens possess typical pseudopolygnathid cavities, it is here included in this genus.

Pseudopolygnathus postinodosus sp. nov.

Plate 6, figs. 6a-c

DERIVATION OF NAME. After the high denticles of the posterior extension of the carina.

DIAGNOSIS. *Pseudopolygnathus* characterized by posterior extension of carina bearing a few high denticles. Platform situated in mid-third of unit bears a few indistinct nodes confined to convex margins. Anterior blade also distinctive, being highest at mid length, sloping abruptly to posterior and more gently to anterior. Basal cavity elongate with thickened lips.

MATERIAL. 3 specimens : Holotype X 496 (figured).

TYPE LOCALITY AND HORIZON. Avon Gorge Z₂ Limestones. Sample Z 38.

RANGE. Avon Gorge Z 13-Z38.

DESCRIPTION. In oral view the platform is seen to occupy the mid third of the unit, the anterior blade the anterior third of the unit, and the posterior extension of the carina the posterior third. The axis is straight to slightly curved and it is possible to recognize right and left forms, although in the present study only right forms have been found. The anterior blade is composed of 7 denticles ; the 3 at the posterior are smaller than the other 4. The fourth anterior denticle is highest and the third anterior denticle is only slightly lower than the fourth. The anterior two denticles are, like the third and fourth, free for the greater part of their length, but they are lower than the third and fourth denticles. The carina in the region of the platform is low and consists of a number of stubby denticles, which are fused together. At the posterior extremity of the platform the denticles of the carina become distinct, and on the posterior extension there are a few distinct high denticles.

In lateral view the denticles of the anterior blade and of the posterior extension of the carina are stout and spine-like. The three denticles of the posterior extension of the carina are free from the base to the tips, and diverge at a wide angle from one another. The anterior edge of the anterior blade and the posterior edge of the

posterior extension of the carina are of equal elevation. The four high anterior denticles of the anterior blade give the anterior edge of the anterior blade a serrated appearance. The low carina is raised slightly above the level of the platform.

The basal cavity is situated in the anterior part of the platform. It has an oval outline, with very thick lips. It is slightly longer than wide and a narrow trough runs from the pit to the posterior extremity of the platform. A keel runs from the anterior extremity of the basal cavity to the anterior extremity of the unit.

REMARKS. It is considered likely that *Pseudopolygnathus postinodosus* sp. nov. developed from *Spathognathodus* sp. nov. by the continued development of a platform, transitional specimens between the two species having been found. In these transitional specimens a second row of nodes is developed on the inner side of the blade, directly over the basal cavity. This development is in addition to the row of nodes on the outer side of the blade (see Fig. 47).

Pseudopolygnathus primus Branson & Mehl

Plate 6, figs. 4a-5c, 710a-12c

- 1934 *Pseudopolygnathus prima* Branson & Mehl : 298, Pl. 24, figs. 24, 25.
 1934 *Pseudopolygnathus foliacea* E. R. Branson : 316, Pl. 26, figs. 27, 28.
 1934 *Pseudopolygnathus irregularis* E. R. Branson : 316, Pl. 26, figs. 25, 26.
 1934 *Pseudopolygnathus corrugata* E. R. Branson : 317, Pl. 26, fig. 23.
 1934 *Pseudopolygnathus costata* E. R. Branson : 317-318, Pl. 26, fig. 21.
 1934 *Pseudopolygnathus distorta* E. R. Branson : 318-319, Pl. 26, figs. 16, 17.
 ? 1934 *Pseudopolygnathus varicostata* E. R. Branson : 318, Pl. 26, figs. 19, 20.
 1934 *Pseudopolygnathus sulcifera* E. R. Branson : 319, Pl. 26, fig. 15.
 1934 *Pseudopolygnathus asymmetrica* E. R. Branson : 320, Pl. 26, fig. 12.
 1934 *Pseudopolygnathus inequicostata* E. R. Branson : 321, Pl. 26, fig. 6.
 1934 *Pseudopolygnathus crenulata* E. R. Branson : 321, Pl. 26, figs. 4, 5, 7, 8.
 1934 *Pseudopolygnathus lobata* E. R. Branson : 322, Pl. 26, figs. 1, 2.
 1938 *Pseudopolygnathus prima* Branson & Mehl ; Branson & Mehl : Pl. 33, figs. 47, 48.
 ? 1938 *Pseudopolygnathus varicostata* E. R. Branson ; Branson & Mehl : 133, Pl. 33, figs. 25, 46.
 1939 *Polygnathus subserrata* Branson & Mehl ; Cooper : 404, Pl. 39, figs. 75, 76 only.
 1939 *Pseudopolygnathus asymmetrica* E. R. Branson ; Cooper : 406-407, Pl. 40, figs. 23, 24, 59, 60, Pl. 41, figs. 13, 14.
 1939 *Pseudopolygnathus crenulata* E. R. Branson ; Cooper : 407, Pl. 40, figs. 25-27.
 ? 1939 *Pseudopolygnathus varicostata* E. R. Branson ; Cooper : 408, Pl. 40, figs. 44, 45.
 1939 *Pseudopolygnathus prima* E. R. Branson & Mehl ; Cooper : 408, Pl. 40, figs. 30, 31.
 1939 *Pseudopolygnathus irregularis* Branson ; Cooper : 408, Pl. 40, figs. 21, 22, 35, 36.
 1939 *Pseudopolygnathus distorta* E. R. Branson ; Cooper : 408-409, Pl. 40, figs. 49-50.
 1944 *Pseudopolygnathus prima* Branson & Mehl ; Branson & Mehl : 244, Pl. 94, figs. 11, 12.
 1944 *Pseudopolygnathus prima* Branson & Mehl ; Branson & Mehl : 181, Pl. 32, figs. 25, 26.
 ? 1944 *Pseudopolygnathus varicostata* E. R. Branson ; Branson & Mehl : 181, 222, Pl. 32, figs. 25, 46.
 1949 *Pseudopolygnathus aurita* Youngquist & Patterson : 67-68, Pl. 16, figs. 5, 6.
 1949 *Pseudopolygnathus carinata* Youngquist & Patterson : 68, Pl. 16, fig. 4.
 1949 *Pseudopolygnathus irregularis* Branson ; Youngquist & Patterson : 68-69, Pl. 16, figs. 1-3.
 1949 *Pseudopolygnathus prima* Branson & Mehl ; Thomas : 412, Pl. 4, fig. 17.

- 1949 *Pseudopolygnathus* cf. *crenulata* E. R. Branson ; Thomas : 412, Pl. 4, fig. 18.
 1949 *Pseudopolygnathus constrictiterminata* Thomas : 428, Pl. 4, fig. 16.
 1949 *Pseudopolygnathus* cf. *P. asymmetrica* E. R. Branson ; Thomas : 436, Pl. 3, fig. 42.
 1951 *Pseudopolygnathus prima* Branson & Mehl ; Hass : 2358, Pl. 1, fig. 11.
 1957 *Pseudopolygnathus prima* Branson & Mehl ; Cloud, Barnes & Hass : 813, Pl. 5, fig. 10.
 1957 *Pseudopolygnathus irregularis* Branson ; Bischoff : 51, Pl. 6, figs. 12, 13.
 1957 *Pseudopolygnathus dentilineata* E. R. Branson ; Bischoff : 50, 51, Pl. 4, fig. 29 only.
 1959 *Pseudopolygnathus prima* Branson & Mehl ; Hass : Pl. 49, fig. 27.
 1959 *Spathognathodus* cf. *costatus* (E. R. Branson) Voges : 298, 299, Pl. 34, fig. 48 only.
 1966 *Pseudopolygnathus prima* Branson & Mehl ; Klapper : 14, Pl. 4, fig. 8.

MATERIAL. 64 specimens : figured, X 546, X 497, X 498, X 499, X 500, X 549.

RANGE. Avon Gorge Z 13-Z 28.

DESCRIPTION. This species is extremely variable. All forms with an asymmetrical platform, a narrow row of nodes or ridges on the right and left sides, but with a flared anterior portion on the left, are referred to it. The basal cavity, according to Klapper, is narrower than the platform, but not all our specimens of *P. primus* agree with this.

The axis is arched, and right and left forms have been found which are bilaterally asymmetrical elements. The platform is more strongly developed on the right side than on the left in both right and left forms. The outer margin of the right side of the platform is convexly curved and bears at least 7 nodes or ridges. The right side of the platform is widest at mid-length, and tapers uniformly to the anterior and posterior. The shorter left side of the platform consists of a smaller number of nodes or ridges than the right side. The carina consists of fused denticles for the greater part of its length, but there are a few distinct denticles at the posterior extremity, where the carina is extended a short distance beyond the posterior end of the platform.

The basal cavity is situated near the mid third of the unit, and is sub-circular in outline with a fold on the inner margin and with a convex outer margin. A narrow groove extends from the anterior extremity of the basal cavity to the posterior extremity of the unit. The anterior edge of the unit, anterior to the basal cavity, is sharp.

REMARKS. *Pseudopolygnathus primus* is similar in outline to *P. dentilineatus*, but the platform ornamentation in the two species is different. The platform ornamentation of *P. primus* has at least seven nodes or ridges on the right side, and ridges are frequently present, whereas in *Pseudopolygnathus dentilineatus* there are nearly always nodes which are confined to the margin ; ridges are rare and eight nodes or ridges on the right side of the platform are unknown. Both margins of the platform in *P. dentilineatus* are convex. In *P. primus* the margin of the left side of the platform is more angular at the anterior than that of *P. dentilineatus*.

The development of *P. primus* has been described by Voges (1959) and again by Klapper (1966). The writers agree with the opinion of Klapper (1966 : 14) that there is a wide variety of surface ornamentation in *P. primus*, but that this can be regarded as intraspecific variation.

P. primus developed from *P. dentilineatus* in the Avonian. Three morphological variations of *P. primus* have been observed: those with a wing-like expansion at the anterior (Pl. 6, fig. 10), those with a considerably larger right side to the platform (Pl. 6, fig. 7) and those where there is a distinct trough on the left side of the anterior part of the platform (Pl. 6, figs. 11, 12). This latter variation closely resembles *P. multistriatus* and becomes the dominant form of *P. primus* in the middle part of the Z Zone.

***Pseudopolygnathus triangulus* cf. *pinnatus* Voges**

Plate 30, fig. 19

- 1959 *Pseudopolygnathus triangula triangula* Voges : 304, 305, Pl. 35, figs. 7-13, p. 297, text-fig. 5 IV.
 1963 *Pseudopolygnathus triangula* subsp. indet Voges ; Ziegler : Pl. 1, figs. 1, 2.
 1963 *Pseudopolygnathus triangula triangula* Voges ; Ziegler : Pl. 1, figs. 3, 4.

MATERIAL. 3 specimens : figured, X 502.

RANGE. Avon Gorge C 7.

DESCRIPTION. This species is characterized by having a platform with a triangular outline. It is straight and wide at the anterior edge of the platform. The platform in oral view is widest slightly anterior to its mid-length. It tapers gradually to the posterior, having straight margins and a triangular posterior outline. Anterior to the mid-length, the margin of the platform is gently curved and it tapers suddenly to the anterior. The anterior blade is broken. The platform is one and a half times as long as wide and has a straight axis. The oral surface of the platform is flat to slightly concave and is ornamented by a number of ridges normal to the margin, which are confined to the outer half of the platform and do not reach the carina. The central carina is strongly developed and has knob-like projections on its upper surface.

The aboral surface is flat and wide. The margins of the outer position are slightly upturned. A strong keel runs the length of the unit, interrupted by the small anteriorly situated pit of the basal cavity.

REMARKS. The specimens found in the present study most closely resemble *Pseudopolygnathus triangula* subsp. indet Ziegler (1963), but the anterior edge of the platform is neither as straight nor as wide as it is in the type specimen (Voges 1959). The present specimens have a more rounded anterior extremity.

***Pseudopolygnathus vogesi* sp. nov.**

Plate 5, figs. 1a-c, 3a-c, 5a-8

- ?1956 *Pseudopolygnathus striata* Mehl & Thomas ; Bischoff & Ziegler : 164, Pl. 11, fig. 20.
 ?1957 *Pseudopolygnathus dentilineata* E. R. Branson ; Bischoff : 50, 51, Pl. 4, figs. 30, 31, 32 only. (non Pl. 4, fig. 29 = *Pseudopolygnathus primus*).
 ?1959 *Pseudopolygnathus dentilineata* E. R. Branson ; Voges : 297, text-fig. 5, fig. 11, Pl. 34, figs. 49, 50.
 ?1964 *Pseudopolygnathus* sp. Bouckaert & Ziegler : 27, Pl. 4, fig. 12.

DERIVATION OF NAME. After Dr. A. Voges.

DIAGNOSIS. Pseudopolygnathid with triangular platform, widest anteriorly, tapering uniformly to pointed posterior. Usually 5 non-marginal bulbous nodes on one side of the platform, and six on the other, confined to the margin. Carina straight or slightly curved, bearing nodes fused towards anterior and free towards posterior. Asymmetrical basal cavity occupying anterior half of platform has fold developed on inner side of unit. Blade low and about equal in length to platform.

MATERIAL. 56 specimens: Holotype X 155, Paratype X 504, X 501, X 505, X 507, X 506 (all figured).

TYPE LOCALITY AND HORIZON. Avon Gorge, lower and middle part of the K Zone. Sample K 12.

RANGE. Avon Gorge K 4-K 14, North Crop KL 1-KL 5.

DESCRIPTION. The axis of the unit is straight or slightly curved. The carina consists of 12 or more nodes, which are fused at the anterior and free at the posterior end. The platform, which is two and a half times as long as its maximum width, is widest anteriorly, there being an abrupt taper to the anterior extremity of the platform. The margins are slightly convex in the anterior third and taper uniformly to the pointed posterior. The posterior tip of the carina continues a short distance beyond the posterior extremity of the platform. The outer side of the platform extends slightly further to the anterior and is also slightly narrower than the other side. It bears up to 5 bulbous nodes, which extend from the margin to the carina; the central node is widest and the anterior two are bigger than the posterior two. The inner side of the platform has up to 6 bulbous nodes, which are smaller than those of the opposite side of the platform. The anterior four nodes do not extend to the carina and are confined to the margin. As a result, there is an anterior trough present in the anterior part of the platform.

The outer side of the asymmetrical basal cavity is convex and the inner side has a fold in the anterior part. The basal cavity is wide and occupies the anterior half of the aboral surface. It is pointed posteriorly and rounded anteriorly. The anterior blade consists of 5 or 6 denticles which are highest at mid-length.

REMARKS. *P. vogesi* occurs in the lower and middle parts of the K Zone in the Avon Gorge. It is a homoeomorph of '*Pseudopolygnathus dentilineata*' E. R. Branson. It resembles *P. dentilineatus* as illustrated by Voges (1959: 297, text-fig. 5, 11) which is characteristic of the lower part of Cu I in West Germany (Bischoff 1957, Voges 1959) and *Pseudopolygnathus* n. sp. of Bouckaert & Ziegler (1965: 27, Pl. 4, fig. 12). In North America, the lowest stratigraphic occurrence of the genus *Pseudopolygnathus* in the Mississippian is the occurrence of *P. dentilineatus* at the base of the Glen Park Formation. *P. dentilineatus* ranges into the lower and middle part of the Hannibal Formation in the Mississippi Valley (Collinson, Scott & Rexroad 1962).

Pseudopolygnathus vogesi sp. nov. is similar to *P. expansus* sp. nov. and transitional specimens have been found.

Pseudopolygnathus sp. A

Plate 6, fig. 3

MATERIAL. 61 specimens : figured, X 515.

RANGE. North Crop ZLA 29-ZLA 32.

DESCRIPTION. The specimen illustrated is very long and narrow. The platform is extremely variable in its development and always highly irregular in outline. Often it consists of irregular nodes rising out of the thickened medial part of the unit ; sometimes these are fused to give a nodose platform of 3 to 4 denticles on either side of the carina. Occasionally there are no nodes on the medial thickening. The carina is very distinctive, consisting of sub-circular needle-like denticles standing high above the platform. The anterior blade is very long and is a continuation of the carina. In aboral view the basal cavity is elongate and asymmetrically flared.

Genus *SCAPHIGNATHUS* Ziegler 19601960 *Scaphignathus* Ziegler : 403.TYPE SPECIES. *Scaphignathus velifera* Ziegler 1960.

The generic name and the type species were used, and the latter described, by Helms (1959 : 655) who referred both to Ziegler 1959 as author. Ziegler's paper was not published until 1960, but subsequent authors have also attributed the genus to him, and we follow this practice, which Article 50 of the Code of Zoological Nomenclature clearly allows.

Scaphignathus ? sp. A

Plate 2, figs. 13a-c

MATERIAL. 1 specimen : figured, X 532.

RANGE. North Crop ZL 2.

DESCRIPTION. The unit is boat-shaped, being asymmetrical with the anterior blade developed on the right hand side when viewed posteriorly. The anterior blade is broken in the only specimen. The platform is lanceolate, being widest at the anterior, and is triangular in cross-section in the posterior portion. It is over twice as long as wide, and is ornamented with low transverse ridges, terminating in low nodes on the platform edge. Along the mid-line there runs a low nodose carina, which joins the inner edge immediately posterior to the outer lateral blade, and then runs as a low ridge anteriorly, joining the outer lateral blade and thus preventing the trough from opening anteriorly.

In aboral view the cavity is large and asymmetrical, being expanded on the inner side : the posterior part of the platform has a keel with a median groove.

REMARKS. This form differs from *Scaphignathus* ? sp. B in that the oral trough does not open anteriorly. The reasons for placing these two forms tentatively in the genus *Scaphignathus* are given in the remarks following the description of *S.* sp. B.

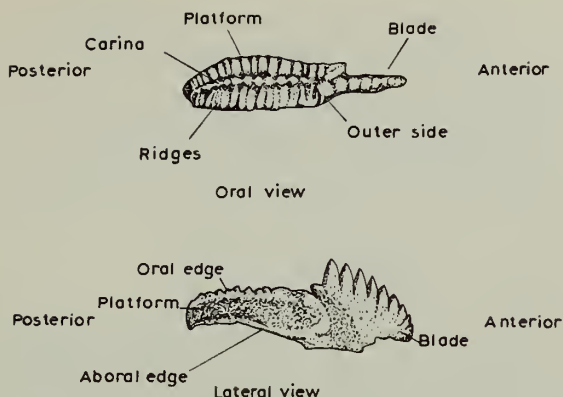


FIG. 44. *Scaphignathus* sp. showing morphological terms used in the text.

Scaphignathus ? sp. B

Plate 2, figs. 12a-c

MATERIAL. 3 specimens : figured, X 533.

RANGE. North Crop ZL 9-ZL 10, Avon Gorge Z 12.

DESCRIPTION. The only specimens present in our faunas have the posterior part of the platform missing. The blade consists of 5 denticles of equal height, situated on the right side of the platform when viewed from the posterior. The outer platform ornament consists of low transverse ridges, giving a crenulate platform, uniting with the inner side immediately posterior to the outer anterior blade, and running as a low, non-denticulate inner blade not quite to the anterior of the unit. It is separated from the outer lateral blade by a sulcus, which deepens anteriorly.

In aboral view the cavity is large and asymmetrical, being expanded on the inner side. The unit is sub-triangular in cross-section and essentially boat-like.

REMARKS. The presence of a median carina precludes the placing of these two species in either *Cavusgnathus* or *Clydagnathus* and the basal cavity differs greatly from the small basal cavity of *Mestognathus*. *Scaphignathus* has a small pit in adult specimens but a large one in juveniles. Our specimens would appear to be adult but are tentatively assigned to that genus.

Genus *SIPHONODELLA* Branson & Mehl

1934 *Siphonognathus* Branson & Mehl : 295 (non Richardson 1858).

1944 *Siphonodella* nom. nov. Branson & Mehl : 245.

TYPE SPECIES. *Siphonognathus duplicata* Branson & Mehl 1934.

Siphonodella isosticha (Cooper)

Plate 12, figs. 9a, b, 11a, b

- 1939 *Siphonognathus isosticha* Cooper : 409, Pl. 41, figs. 9, 10.
 1962 *Siphonodella* n. sp. A Collinson, Scott & Rexroad : 7, fig. 4.
 1962 *Siphonodella obsoleta* Cooper ; Müller (*partim*) : 1388, fig. 4 only.
 1964 *Siphonodella isosticha* (Cooper) Rexroad & Scott : 44, Pl. 3, figs. 21-23.
 1965 *Siphonodella isosticha* (Cooper) Ethington : 587, Pl. 67, figs. 15, 17.

MATERIAL. 3 specimens : figured, X 534, X 535.

RANGE. North Crop KL 16-KL 19.

DESCRIPTION. The platform is narrow and elongate being broadest at its mid-point. Ornament is lacking except for a medial nodose carina, two short anterior rostral ridges, a few scattered nodes on the narrow inner platform, and incipient transverse denticles on the margin of some specimens (Pl. 12, fig. 11a). The basal cavity is minute, and the whole unit keeled.

REMARKS. Rexroad & Scott (1964 : 44) suggested that this species arose from *S. obsoleta* Hass by reduction of the outer rostral ridge and platform ornament, but they pointed out that the juveniles of the two species are very similar. All our specimens appear to be young forms and they could be assigned either to *S. obsoleta* or *S. isosticha*, but absence of platform ornament in the largest specimen suggests that they should be placed in *S. isosticha*.

Siphonodella obsoleta Hass

Plate 12, figs. 13a-c

- 1959 *Siphonodella obsoleta* Hass : 392, Pl. 47, figs. 1, 2.
 1962 *Siphonodella* aff. *S. obsoleta* Hass ; Collinson, Scott & Rexroad : 7, chart 2.
 1964 *Siphonodella obsoleta* Hass ; Rexroad & Scott : 45, Pl. 3, fig. 25.
 1964 *Siphonodella obsoleta* Hass [Nass in text] ; Budurov & Tschurnev : Pl. V, figs. 5a-c, 11a, b, 13a, b, 14-17, 19.

MATERIAL. 2 specimens : figured, X 536.

RANGE. North Crop KL 16-KL 19.

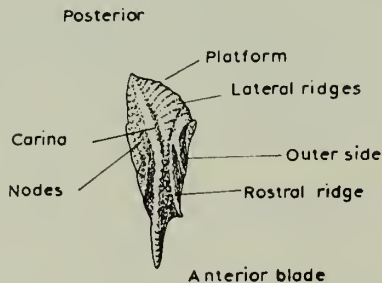


FIG. 45. *Siphonodella* sp. showing morphological terms used in the text.

DESCRIPTION. The long outer rostral ridge distinguishes this species from *S. isosticha* (Cooper). The ridge is situated on the outer platform and curves away from the carina, paralleling the platform margin. It degenerates into a line of low isolated nodes before becoming obsolescent near the posterior termination. The inner platform bears irregular low nodes over the whole surface.

Siphonodella sp. A

Plate 12, figs. 12a, b

MATERIAL. 1 specimen : figured, X 537.

RANGE. North Crop KL 16.

DESCRIPTION. This specimen is a siphonodellid with a rounded posterior margin, and a lobe developed on the posterior part of the outer side. The inner platform possesses two longitudinal rostral ridges in its anterior part, the posterior part being expanded laterally and ornamented with irregular low nodes, three of which replace the carina, while others spread on to the outer platform. The outer platform possesses a long rostral ridge, which covers the length of the platform and extends along a lobe situated in the posterior part. The platform is unornamented except for isolated nodes in the posterior.

In aboral view the unit is relatively flat and possesses a minute siphonodellid cavity.

REMARKS. This specimen is unlike any other described siphonodellid species. It may be a pathologic variant of *S. obsoleta* Hass.

Siphonodella sp.

Plate 31, fig. 20

MATERIAL. 2 specimens : figured, X 539.

RANGE. Avon Gorge K 12-K 17.

DESCRIPTION. Two fractured specimens of the genus *Siphonodella* were found in the Upper K Zone Beds. One specimen consists of the anterior quarter of the platform, and the other of the anterior quarter of the platform and the anterior blade. One of the specimens has one rostral ridge and the other two rostral ridges, developed on either side of the carina. It is not possible to refer the specimens to any species.

Genus *SPATHOGNATHODUS* Branson & Mehl 1941

- 1856 *Ctenognathus* Pander (*partim*) : 32 (*non Ctenognathus* Fairmaire 1843).
 1933 *Spathodus* Branson & Mehl : 41 (*non Spathodus* Boulenger 1900).
 1940 *Pandorina* Stauffer 428 (*non Pandorina* Bory de St. Vincent 1827, *nec* Scacchi 1833).
 1941 *Spathognathodus* nom. nov. Branson & Mehl : 98, (*pro Spathodus* Branson & Mehl 1933).
 1945 *Mehlina* Youngquist : 363.
 1957 *Ctenognathus* (*Pandorinellina*) Müller & Müller : 1083.
 1959 *Pandorinellina* Hass 378, (*pro Pandorina* Stauffer 1940).
 1959 *Branmehla* Hass 381.

- 1959 *Ctenognathodus* nom. nov. Fay : 195 (*pro Ctenognathus* Pander 1856).
 1959 *Ctenognathus* (*Ctenognathodus*) Fay : 195.
 1959 *Ctenognathodus* (*Mehlina*) Fay 195.
 1962 *Spathognathodus* (*Bispathodus*) Müller : 114.

TYPE SPECIES. *Ctenognathus murchisoni* Pander 1856.

The name *Pandorinellina* was first used by Müller & Müller (1957 : 1083) but was clearly attributed by them to Hass in the (then forthcoming) Treatise. Article 50 of the Code of Zoological Nomenclature justifies the attribution of the genus to Hass.

Spathognathodus anteposicornis Scott

Plate 3, figs. 5a-8b

- 1961 *Spathognathodus* n. sp. A Scott & Collinson : 132, Pl. 1, figs. 12-15.
 1961 *Spathognathodus anteposicornis* Scott : 1224, text-fig. 2H - K.

MATERIAL. 59 specimens : figured, X 540, X 541, X 542, X 543.

RANGE. North Crop KL 19-ZLA 15, Avon Gorge K₂ 1-Z 28.

DESCRIPTION. The unit is elongate, being two to three times as long as the highest anterior denticles ; it is straight in oral view, and highest at the anterior. The anterior 3 denticles are the largest, standing twice as high as the remaining blade denticles, the medial denticle of the three usually being highest. The remaining denticles are of equal height over the medial third, gradually decreasing in size posteriorly over the posterior third ; they are erect, basally fused and blunt tipped. The aboral edge is straight (Pl. 3, fig. 5a) to gently arched (Pl. 3, fig. 7a). A lateral denticle, sub-circular in cross-section, is developed high on the inner side of the unit over the anterior portion of, or immediately anterior to, the basal cavity, the tip generally being about equal in height to the adjacent denticles of the blade.

In aboral view the basal cavity is large and flaring, with an anterior pit. The cavity occupies the median third and extends in both directions as an aboral groove. The outer margin of the cavity is subcircular (Pl. 3, fig. 5b) to biconvex (Pl. 3, fig. 6b).

REMARKS. Scott (1961 : 1224) described this species from the Louisiana Limestone, which he regarded as Upper Devonian. Our specimens, which have a restricted range above the Avonian occurrence of the genus *Siphonodella*, would appear to be stratigraphically younger. Their occurrence in the present faunas may be the result of one or more of at least three different factors : an independent phylogenetic origin, so that they are homoeomorphs of Scott's *S. anteposicornis* : a greater stratigraphic range for that species than has been hitherto supposed : or a Lower Carboniferous age for the Louisiana Limestone. Without firm evidence in support of any one interpretation, it seems preferable to assign the present specimens to *S. anteposicornis* Scott.

One feature of the stratigraphically older specimens of this species (Pl. 3, fig. 6a), is the prominent square antero-aboral angle of the blade, and the posterior inclination of the three large anterior denticles. These features, though present, are less marked in stratigraphically younger specimens (e.g. Pl. 3, fig. 7a). There also seems to be an

anterior migration of the lateral denticle in stratigraphically younger specimens in the present faunules, but the samples are too small to justify any firm conclusion.

Spathognathodus bischoffi sp. nov.

Plate 4, figs. 1a-4c

- 1956 *Spathognathodus costatus* (E. R. Branson) Bischoff & Ziegler : 166, Pl. 13, fig. 3.
 1957 *Spathognathodus costatus* (E. R. Branson) Bischoff : 56, Pl. 4, fig. 28.
 1957 *Spathognathodus costatus* (E. R. Branson) Ziegler in Flügel & Ziegler ; Pl. 1, figs. 15, 18 only.
 1959 *Spathognathodus costatus* (E. R. Branson) Helms : Pl. 111, figs. 2-4.
 1959 *Spathognathodus costatus* (E. R. Branson) Voges : 297, text-fig. 5, fig. 1.
 1962 *Spathognathodus costatus costatus* (E. R. Branson) Ziegler : 107, 108, Pl. 14, figs. 1-6, 8-10.

DERIVATION OF NAME. In honour of Dr. G. Bischoff.

DIAGNOSIS. Elongate spathognathodid with, a greatly laterally expanded pseudopolygnathid-type basal cavity, a central oral blade of very uniform, confluent, blunted denticles, and a series of about twelve strong, low, regular, laterally-elongate nodes developed along whole inner length of unit except for anterior blade. Outer oral surface of cup may be feebly nodose.

MATERIAL. 10 specimens : Holotype X 401, Paratypes (all figured) X 398, X 400, X 399.

TYPE LOCALITY AND HORIZON. Hönnetal, West Germany to VI Zone-Upper *costatus* Zone, Roadside cutting (Ziegler 1962).

DESCRIPTION. These elongate spathognathodids have an anterior blade two to three times as deep as the posterior end of unit. The anterior blade consists of about 3 to 4 confluent, but apically discrete denticles, their apices being bluntly pointed. The anterior edge is straight and deep, making an angle of 80°-90° with the aboral

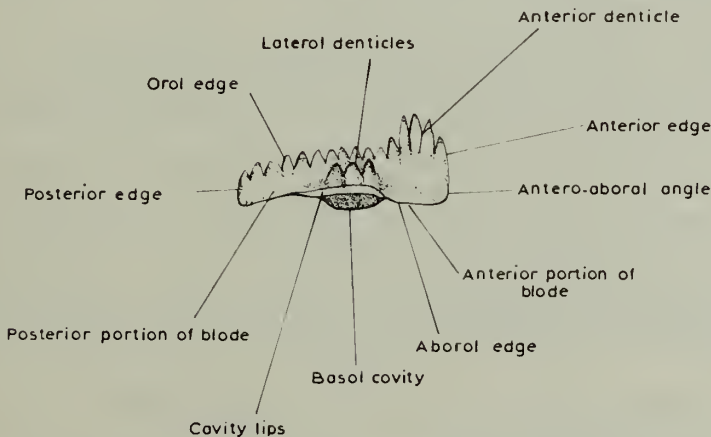


FIG. 46. *Spathognathodus* sp. showing morphological terms used in the text.

edge, the antero-aboral angle being bluntly rounded to angular and conspicuous. The median denticles, posterior to the blade, are confluent for their whole length, their individual tips being only rarely discernible. Those in the median two-thirds of the unit are of uniform height, the posterior ones being shorter, and having 4 to 6 conspicuous apices.

The basal cavity is longitudinally restricted but makes a conspicuous feature in lateral view.

In oral view, the blade is seen to be gently curved in a horizontal plane, although only left forms are known. The denticles are conspicuously laterally expanded to give a platform-like appearance to the whole unit. The size of the platform increases during ontogeny (cf. Pl. 4, figs. 1a & 4a). There are up to 14 transverse denticles developed, those near mid-length being the widest, giving the platform a general biconvex outline in oral view. Deep transverse troughs separate the denticles, and there is a tendency for a feeble longitudinal trough to develop also.

In aboral view the asymmetrical laterally expanded basal cavity is a conspicuous feature, both its lateral expansion and its asymmetry increasing in ontogeny. Its transverse axis lies obliquely to the longitudinal axis of the unit, the outer (convex) extension pointing more posteriorly. It extends to the posterior end of the unit as a deep and wide but gradually narrowing cavity, and as a slit-like groove along the anterior part of the blade.

Spathognathodus coaptus (Branson & Mehl)

Plate 7, figs. 9a–11c

- 1934 *Spathodus coaptus* Branson & Mehl : 275, Pl. 22, fig. 16.
 1938 *Spathodus elongatus* Branson & Mehl (*partim*) : 139, Pl. 23, fig. 6 only.
 1939 *Spathodus crassidentatus* Branson & Mehl ; Cooper : 413, Pl. 45, fig. 19.
 1939 *Spathodus aciedentatus* E. R. Branson ; Cooper : 413, Pl. 45, figs. 26, 28, 44.
 1939 *Spathodus chouteauensis* Cooper : 413, Pl. 45, fig. 20.
 1939 *Spathodus isus* Cooper : 413, Pl. 45, fig. 33.
 1939 *Spathodus strigilis* Huddle ; Cooper : 416, Pl. 45, fig. 37.
 1939 *Spathodus sulciferus* Branson & Mehl ; Cooper : 416, Pl. 45, figs. 17, 18.
 1949 *Spathognathodus sulciferus* (Branson & Mehl) Youngquist & Patterson : 72, Pl. 15, fig. 1.
 1949 *Spathognathodus crassidentatus* (Branson & Mehl) Youngquist & Patterson : 71, Pl. 15, fig. 2.
 1949 *Spathognathodus aciedentatus* (E. R. Branson) Youngquist & Patterson : 17, Pl. 15, fig. 3.
 ? 1949 *Spathognathodus aciedentatus* (E. R. Branson) Thomas : 412, Pl. 4, fig. 7.
 1951 *Spathognathodus macer* (Branson & Mehl) Youngquist & Downs : 791, Pl. 3, figs. 1, 2.
 1958 *Spathognathodus crassidentatus* Branson & Mehl ; Freyer : 85, Pl. 6, fig. 138.
 1964 *Spathognathodus crassidentatus* Branson & Mehl ; Rexroad & Scott : 48, Pl. 3, figs. 7, 8.

MATERIAL. 68 specimens : figured, X 453, X 454, X 436.

RANGE. Avon Gorge Z 1–Z 38.

DESCRIPTION. This is a straight bladed spathognathodid, with a straight aboral

edge. The 3 or 4 anterior denticles are higher than those of the rest of the blade. The number of oral denticles is variable but averages 15. The denticles of the oral edge are of uniform elevation with the exception of the posterior two or three, which may be slightly lower. The basal cavity is situated at the mid-length of the unit and is circular in outline.

The denticles of the oral edge are of fairly uniform elevation, with the exception of those at the posterior tip, which are slightly lower, and those at the anterior, which rise gradually to form an anterior blade. The anterior and posterior edges are straight, and form right angles with the aboral edge. The aboral edge is straight. The basal cavity is sub-circular in outline and centrally situated.

REMARKS. *Spathognathodus coaptus* closely resembles *S. crassidentatus* and *S. denticulatus*. In *S. crassidentatus* the aboral edge is arched in the posterior two thirds. In *S. denticulatus* the basal cavity is narrow and elongate.

Spathognathodus costatus costatus (E. R. Branson)

Plate 3, figs. 13a-15b

- 1934 *Spathodus costatus* E. R. Branson : 303, Pl. 27, fig. 13.
 1938 *Spathodus costatus* E. R. Branson ; Branson & Mehl : 132, 136, Pl. 33, fig. 1.
 1944 *Spathodus costatus* E. R. Branson ; E. B. Branson : 181, Pl. 32, fig. 1.
 ? 1949 *Spathognathodus costatus* (E. R. Branson) Thomas : 409, 412, Pl. 4, fig. 10.
 non 1956 *Spathognathodus costatus* (E. R. Branson) Bischoff & Ziegler : 166, Pl. 13, fig. 3.
 non 1957 *Spathognathodus costatus* (E. R. Branson) Bischoff : 56, Pl. 4, fig. 28.
 non 1957 *Spathognathodus costatus costatus* (E. R. Branson) ; Ziegler in Flügel & Ziegler : Pl. 1, figs. 15, 18 only.
 non 1959 *Spathognathodus costatus* (E. R. Branson) Helms : Pl. 111, figs. 2-4.
 non 1959 *Spathognathodus costatus* (E. R. Branson) Voges : 297, text-fig. 5, fig. 1.
 non 1959 *Spathognathodus* cf. *costatus* (E. R. Branson) Voges : 297, Pl. 34.
 non 1962 *Spathognathodus costatus costatus* (E. R. Branson) Ziegler : 107, 108, Pl. 14, figs. 1-6, 8-10.
 ? 1964 *Spathognathodus costatus costatus* (E. R. Branson) Higgins, Wagner-Gentis & Wagner : Pl. 5, fig. 21.

MATERIAL. 170 specimens : figured, X 455, X 166, X 456.

RANGE. North Crop ZLA 2-ZL 10, Avon Gorge K 18-Z 28.

DESCRIPTION. The unit is slightly arched and bowed, being highest at the anterior end, although the anterior blade is only about one third as high again as the posterior end. The oral profile is sigmoidal, the anterior blade being highest and consisting of 3 or 4 large denticles, the tallest of which is either the anterior-most or penultimate anterior denticle. The denticles of the mid-region are of equal height, and lower than the anterior denticles, and the unit shallows posteriorly. Situated on the inner side of the unit is a row of peg-like nodes, 5 to 8 in number, which tend to jut out of the unit. These nodes may be joined to the main unit by transverse ridges, but these ridges lie below the level of the node tips.

In aboral view the cavity occurs in mid-length, is fairly large and symmetrical, and is widest at its mid-point. It extends as a narrow groove to near the posterior termination and for a short distance along the anterior blade.

Spathognathodus costatus sulciferus (Branson & Mehl)

Plate 3, figs. 16a-18c

- 1934 *Spathodus sulciferus* Branson & Mehl : 274, Pl. 22, figs. 12, 13.
 1934 *Spathodus spinulicostatus* E. R. Branson : 305, Pl. 27, fig. 19.
 1938 *Spathodus spinulicostatus* E. R. Branson ; Branson & Mehl : 132, Pl. 33, fig. 2.
 non 1939 *Spathodus sulciferus* Branson & Mehl ; Cooper : 416, Pl. 45, figs. 17, 18 (fig. 17 = *S. cyrius*, fig. 18 = *S. crassidentatus*).
 1944 *Spathodus spinulicostatus* E. R. Branson ; E. B. Branson Pl. 32, fig. 2.
 1944 *Spathognathodus sulciferus* (Branson & Mehl) Branson & Mehl in Shimer & Shrock : Pl. 94, fig. 2.
 ? 1961 *Spathognathodus costatus spinulicostatus* (E. R. Branson) Higgins, Wagner-Gentis & Wagner : Pl. 5, fig. 22.

MATERIAL. 29 specimens : figured, X 457, X 458, X 459.

RANGE. North Crop ZLA 4-ZL 10, Avon Gorge K 18-Z 26.

DESCRIPTION. The unit is straight, very slightly arched and highest at the anterior end. The anterior blade consists of 3 to 4 high denticles, its oral outline being gently convex upward. The medial part of the unit possesses denticles of equal height, the posterior part having denticles which become progressively lower toward the posterior termination. Both lateral faces of the unit bear nodes, the inner row of about 10 being similar to the inner row of *S. costatus costatus*, with the largest nodes lying in the medial position and having depressed and inconspicuous transverse connecting ridges. The outer lateral dentition is confined mainly to the area of the oral side of the cavity lip and consists of 1 to 3 large fused nodes of lower height than the inner row. The posterior part of the outer face occasionally bears isolated denticles (Pl. 3, fig. 16).

In aboral view the cavity is large, medial and sub-symmetrical, tending to have a greater amount of flaring on the outer side ; it is about twice as long as wide and runs posteriorly as a narrow groove. It is laterally expanded, and wider at the anterior end.

REMARKS. *S. costatus sulciferus* is obviously very closely related to *S. costatus costatus*, differing only in the addition of lateral denticles on the outer side. Further enlargement of the outer platform gives species referable to the genus *Pseudopolygnathus*, although that genus is polyphyletic.

Spathognathodus crassidentatus (Branson & Mehl)

Plate 3, figs. 1a-4b

- 1934 *Spathodus crassidentatus* Branson & Mehl : 276, Pl. 22, figs. 17, 18.
 1934 *Spathodus crassidentatus* Branson & Mehl ; E. R. Branson : 303, Pl. 27, fig. 12.
 1934 *Spathodus denticulatus* E. R. Branson : 305, Pl. 27, fig. 17.
 1934 *Spathodus aciedentatus* E. R. Branson : 306, Pl. 27, figs. 21, 23.
 1934 *Spathodus strigilis* Huddle : 89, Pl. 7, fig. 15 ; Pl. 12, fig. 11.
 1934 *Spathodus parvus* Huddle : 90, Pl. 7, fig. 16.
 1938 *Spathodus crassidentatus* Branson & Mehl ; Branson & Mehl : 132, 137, Pl. 33, fig. 5.
 1938 *Spathodus elongatus* Branson & Mehl (*partim*) : 139, Pl. 34, fig. 9 (*non* Pl. 34, fig. 6 = *S. elongatus*).

- 1939 *Spathodus crassidentatus* Branson & Mehl ; Cooper : 413, Pl. 45, fig. 19.
 1939 *Spathodus acidentatus* E. R. Branson ; Cooper : 413, Pl. 45, figs. 26, 28, 44.
 1939 *Spathodus chouteauensis* Cooper : 413, Pl. 45, fig. 20.
 1939 *Spathodus strigilis* Huddle ; Cooper : 416, Pl. 45, fig. 37.
 1939 *Spathodus sulciferus* Branson & Mehl ; Cooper (*partim*) : 416, 420, Pl. 45, fig. 18.
 1939 *Spathodus isus* Cooper : 413, Pl. 45, fig. 33.
 1943 *Spathodus strigilis* Huddle ; Cooper & Sloss : 175, Pl. 28, figs. 3, 4, 10, 12.
 1943 *Spathognathodus crassidentatus* (Branson & Mehl) Cooper & Sloss : 175, Pl. 28, fig. 1.
 1949 *Spathognathodus crassidentatus* (Branson & Mehl) Youngquist & Patterson : 71, Pl. 15, fig. 2.
 1949 *Spathognathodus acidentatus* (E. R. Branson) Youngquist & Patterson : 71, Pl. 15, fig. 3.
 1949 *Spathognathodus quintidentatus* Thomas : 429, Pl. 4, figs. 8, 9.
 1949 *Spathognathodus acidentatus* (E. R. Branson) Thomas, Pl. 4, fig. 7.
 1956 *Spathognathodus crassidentatus* (Branson & Mehl) Bischoff & Ziegler (*partim*) : 166, Pl. 13, fig. 14 (*non* Pl. 13, fig. 13).
 1957 *Spathognathodus crassidentatus* (Branson & Mehl) Bischoff : 56.
 1961 *Spathognathodus crassidentatus* (Branson & Mehl) Freyer : 85, Pl. 6, fig. 138.
 1964 *Spathognathodus crassidentatus* (Branson & Mehl) Rexroad & Scott : 48, Pl. 3, figs. 7, 8.

MATERIAL. 222 specimens : figured, X 460, X 461, X 462, X 463.

RANGE. North Crop KL 2-ZLA 33, Avon Gorge K 17-Z 38.

DESCRIPTION. This is a simple arched and bowed unit, which is highest at the anterior. The anterior blade consists of 3 to 6 tall, massive denticles which are basally confluent, with discrete blunt apices, the denticles in the medial part of the blade being highest. The mid-third of the unit consists of denticles of even height, conspicuously lower than the anterior denticles. The denticles of the posterior third decrease in height towards the posterior termination. The total number of denticles ranges from 17 to 22.

In aboral view a large cavity, situated medially, is symmetrically flared and widest just anterior to its mid-point. The cavity is extended both anteriorly and posteriorly as a narrowing groove, the posterior extension being the longer.

REMARKS. This species is common, and, as was pointed out by Rexroad and Scott (1964 : 49), is highly variable. Although we accept most of the synonymy of those authors, we believe that forms with a very much greater denticle density should not be included under *S. crassidentatus*, but should be referred to *S. cyrius* (Cooper) (see p. 234).

Spathognathodus cristulus Youngquist & Miller

Plate 8, figs. 14a-18d

- 1949 *Spathognathodus cristula* Youngquist & Miller : 621, Pl. 101, figs. 1-3.
 1957 *Spathognathodus cristula* Youngquist & Miller ; Rexroad : 38, Pl. 3, figs. 16, 17.
 1958 *Spathognathodus cristula* Youngquist & Miller ; Rexroad : 25, Pl. 6, figs. 3, 4.
 1961 *Spathognathodus cristula* Youngquist & Miller ; Rexroad & Burton : 1156, Pl. 141, fig. 9.
 1962 *Spathognathodus cristula* Youngquist & Miller ; Rexroad & Liebe : 511, table 1.
 1964 *Spathognathodus cristula* Youngquist & Miller ; Rexroad & Furnish : 674, Pl. 111, fig. 15.
 1965 *Spathognathodus cristula* Youngquist & Miller ; Rexroad & Nicoll : 26, Pl. 1, figs. 1, 2.

MATERIAL. 278 specimens : figured, X 464, X 465, X 466, X 467, X 468.

RANGE. North Crop CYD 7, Avon Gorge Z 1-D 26.

DESCRIPTION. This spathognathodid bears 8 to 12 denticles along its oral edge, of which the most anterior is the largest. The remaining denticles decrease uniformly in size towards the posterior end, so that the general form of the denticulate edge is continuously convex, being lowest posteriorly. The basal cavity extends for about two-thirds the length of the unit. It is widest at the anterior end, and is continuous to the posterior end, being biconvex in outline.

The short blade is distinguished by a deep anterior end, with a high anterior denticle. The anterior edge of the unit slopes conspicuously forward so that its antero-aboral projection lies in front at the tip of the denticle. The antero-aboral angle is either bluntly rounded or more or less angular, forming an angle of about 90°. The anterior edge is straight. The anterior denticle is about half as long again as that adjacent to it, and about twice as wide. The remaining denticles of the bar decrease uniformly in size towards the posterior end. Except for the two posterior denticles which tend to be conspicuously smaller than the rest, the denticles are discrete only at their bluntly rounded tips. They have convex lateral faces and stand erect to the bar. The posterior margin, which is formed of the two most posterior denticles, tends to slope posteriorly. In lateral view the aboral edge of the unit is straight in the anterior third of the unit, but is concave posteriorly, because of the flare of the basal cavity. This cavity is slightly asymmetrical, but is strongly convex in outline and extends for about two thirds the length of the aboral surface. Its maximum width is only about half or a third of its total length and its greatest depth and width are anterior. It extends anteriorly as a median slit along the anterior blade.

There is a tendency in some specimens for the posterior denticles to be progressively posteriorly inclined towards the posterior end. In some specimens the anterior aboral angle is rather less than 90° and the apical denticle is more sharply triangular in lateral view than in other specimens.

REMARKS. The first stratigraphic occurrence of *Spathognathodus cristulus* in the Avonian of the Bristol area is considerably older than that known in other parts of the world.

Spathognathodus elongatus (Branson & Mehl)

Plate 7, figs. 1a-5b

1938 *Spathodus elongatus* Branson & Mehl : 139, Pl. 34, fig. 6 (*non* Pl. 34, fig. 9 = *S. crassidentatus?*).

1944 *Spathodus elongatus* Branson & Mehl ; E. B. Branson : Pl. 39, fig. 6, (*non* Pl. 39, fig. 9 = *S. crassidentatus?*).

MATERIAL. 48 specimens : figured, X 472, X 473, X 474, X 475.

RANGE. North Crop KL 19-ZL 8, Avon Gorge K 4-Z 13.

DESCRIPTION. The blade is straight or gently curved in oral view, being long and

shallow over the whole length. The denticles are highest at the anterior end, decreasing in height towards the position of the anterior end of the cavity, beyond which they increase in size towards the posterior end of the cavity, and then decrease gradually towards the posterior end of the unit. The denticles are compressed, fused at their bases, and free at their tips; about 20 in number. Longitudinal 'shoulders' are developed on the lateral faces below the bases of the denticles. The aboral outline is straight to slightly arched. The very shallow depth of the blade just anterior to the basal cavity gives a 'sagging' profile to the unit. The length of the unit is about four times the maximum depth.

The cavity is symmetrical, elongate and shallow, with a slight appearance of cups. It narrows to grooves at both ends, which extend about halfway along aboral edges towards anterior and posterior ends.

REMARKS. Our specimens agree perfectly with the figured holotype of *S. elongatus* (Branson & Mehl, 1938A, Pl. 34, fig. 6), although their description is scarcely adequate to distinguish this from other species. Within our fauna there appear to be two forms; the first includes those with free standing fine denticles (Pl. 7, fig. 5a) which tend to be sharper, longer and of more regular length than those of the second group, which have laterally compressed denticles (Pl. 7, fig. 1a). The long, free-standing denticles of this first group are reminiscent of *S. denticulatus* (E. R. Branson) (1934, Pl. 27, fig. 17), but the differences in relative length of the units and anterior dentition preclude us from placing these forms within that species. Cooper (1939 : 413) refers the paratype (Pl. 34, fig. 9) to a new species *S. chouteauensis*. Rexroad & Scott (1964 : 48) refer both the holotype and paratype to *S. crassidentatus* (Branson & Mehl). It is possible that the paratype, referred to *S. chouteauensis* by Cooper, is referable to *S. crassidentatus* (Branson & Mehl) but the holotype is definitely a separate species.

***Spathognathodus plumulus plumulus* sp. et subsp. nov.**

Plate I, figs. 1a-2c, 5, 6

DERIVATION OF NAME. From the plume-like anterior blade.

DIAGNOSIS. Spathognathodid with plume-like anterior blade, denticles of which decrease rapidly in size anteriorly from a massive denticle at posterior end of blade. Series of lateral nodes present, developed on the outer side only, above the basal cavity.

MATERIAL. 442 specimens : Holotype X 476, Paratypes X 379, X 380, X 381 (all figured).

TYPE LOCALITY AND HORIZON. R. Clydach, Nr. Gilwern, K Zone North Crop. Sample KL 4.

RANGE. North Crop KL 1-KL 16, Avon Gorge K 2-K₂ 1.

DESCRIPTION. The blade is plume-like in anterior third, consisting of 3 to 6 denticles, decreasing rapidly in height anteriorly from a tall massive denticle situated immediately anterior to the basal cavity. The remainder of the unit is low, consist-

ing of about 16 fused, laterally compressed denticles, those in the posterior third of the unit tending to be the largest. The oral profile, posterior to the blade, is gently convex. Lateral denticles are developed on the outer side above the basal cavity and number from 2 to 5; they tend to form a short platform, restricted to the region of the basal cavity, rather than occurring as laterally divergent peg-like denticles. The aboral lateral profile is conspicuously straight, being arched behind the cavity.

In aboral view the cavity is ovate, slightly asymmetrical, the flared side being the narrower. The long axis is parallel to the long axis of the unit, equal to, or only slightly greater than, the maximum lateral width of the cavity. The cavity may extend as a faint groove for a short distance along the anterior and posterior blades.

REMARKS. Ziegler (1960A, Pl. 3, figs. 8, 9) described forms referred by him to *S. tridentatus*, which appear to be referable to *S. plumulus plumulus*. The form figured by him (1960A, Pl. 3, fig. 7) as *S. sulciferus* is distinct from Branson & Mehl's type specimen which is, in fact, a senior synonym of *S. spinulicostatus* (E. R. Branson 1934). Ziegler's specimen appears from its tall blade and the nature of the anterior face to be closely related to *S. plumulus plumulus*, but its lack of platform development precludes its inclusion in that species, although it may be a form ancestral to spathognathodids with high plume-like blades.

S. plumulus plumulus is probably ancestral to *Clydagnathus* (see p. 85). The lateral profile of the blade, with its sharply descending oral surface, short anterior edge, and rounded antero-aboral angle, is also very similar to that of *Scaphignathus*.

***Spathognathodus plumulus nodosus* sp. et subsp. nov.**

Plate 1, figs. 3a-4c

DERIVATION OF NAME. From the additional nodes on the inner side of cup.

DIAGNOSIS. Subspecies of *S. plumulus* with one or more nodes developed on inner platform expansion.

MATERIAL. 14 specimens: Holotype X 382, Paratype X 383.

TYPE LOCALITY AND HORIZON. R. Clydach, Nr. Gilwern, Lower K Zone North Crop. Sample KL 2.

RANGE. North Crop KL 1-KL 6, Avon Gorge K-8.

DESCRIPTION. This form is similar to *S. plumulus plumulus* in gross morphological detail, but the inner oral lip of the expanded cavity bears one or more nodes.

REMARKS. As in the *S. tridentatus* group, the *S. plumulus* group develops lateral denticles on the inner and outer lateral margins of the cup. In *S. plumulus nodosus* the development towards a pseudopolygnathid morphology (as in the *S. aculeatus* and *S. tridentatus* groups) is seen. The development of the denticle ranges from weak to strong.

***Spathognathodus plumulus shirleyae* subsp. nov.**

Plate 1, figs. 7a-8c

DERIVATION OF NAME. After Mrs. Shirley Osborn.

DIAGNOSIS. Spathognathodid with plume-like anterior blade, having one node developed on outer lateral face above basal cavity.

MATERIAL. 10 specimens : Holotype X 384, Paratype X 385 (both figured).

TYPE LOCALITY AND HORIZON. R. Clydach, Nr. Gilwern, Lower K Zone North Crop. Sample KL 2.

RANGE. North Crop KL 2–KL 3, Avon Gorge K 4–K 8.

DESCRIPTION. The blade is short and thin, the anterior part consisting of a posterior high, massive, recurved, laterally compressed denticle, and the denticles rapidly decreasing in height anteriorly, to give a plume-like effect. The medial and posterior parts of the unit consist of low, fused, laterally compressed, erect to slightly posteriorly inclined denticles. Above the anterior part of the outer cavity lip, a single lateral node denticle arises, which is sub-circular in cross-section.

In aboral view the cavity is elliptical, slightly flared and its long axis is concordant with the long axis of the unit.

REMARKS. This form appears to occupy the same position within the *S. plumulus* lineage as does *S. anteposicornis* Rexroad & Scott within the *S. tridentatus* lineage. The small size of all the present specimens might be interpreted to mean that they are a growth stage of *S. plumulus plumulus* sp. nov., but the presence of three denticles in specimens of that species of comparable small size (Pl. 1, fig. 6) and the restricted range of the present subspecies appear to justify its recognition as distinct.

Spathognathodus pulcher (Branson & Mehl)

Plate 4, figs. 9a–11c

1938 *Spathodus pulcher* Branson & Mehl : 139, Pl. 34, figs. 7, 8.

MATERIAL. 59 specimens : figured, X 386, X 512, X 513.

RANGE. North Crop KL 19–ZLA 15, Avon Gorge Z 12–C 7.

DESCRIPTION. The blade is long and thin, being highest at the anterior and decreasing gradually to a point anterior to the basal cavity, where the profile becomes straight, sloping off abruptly at the posterior termination. The 14 to 15 sub-circular denticles are erect, short, fused at the bases, and free at the sharply pointed tips. The cavity is elongate, expanded, and occurs in the posterior half of the unit, terminating immediately anterior to the posterior end. The anterior part of the blade is about twice as deep as the posterior.

REMARKS. This form differs from *S. crassidentatus* s.s., in the lack of a distinct high blade at the anterior end, and in the posterior (rather than medial) position of the basal cavity. It resembles *S. elongatus* in the anterior half, but the sudden termination immediately posterior to the basal cavity is distinctive (Branson & Mehl 1938A : 139–140, Pl. 34, figs. 7, 8). It is very similar to a form described by Branson & Mehl (1938A) as *S. elongatus* (Pl. 34, fig. 9) which was referred by Cooper (1939) to a new species, *S. chouteauensis*. Rexroad & Scott (1964) refer this to *S. crassidentatus*, but it would appear not to fit even their broad terms for the species. The present specimens are also close to *S. stabilis*.

Spathognathodus scitulus (Hinde)

Plate 8, figs. 9a-11d

1900 *Polygnathus scitulus* Hinde : 343, Pl. 9, figs. 9-11 only.1928 *Panderodella scitula* (Hinde) Holmes : 16, Pl. 6, figs. 26, 28 only.1960 *Spathognathodus scitulus* (Hinde) Clarke : 21, Pl. 3, figs. 12, 13.1962 *Spathognathodus scitulus* (Hinde) Rexroad & Collinson : 20, Pl. 2, figs. 14, 19, 29-31.

MATERIAL. 19 specimens : figured, X 391, X 392, X 393.

RANGE. North Crop CYD 6-3D 14/15, Avon Gorge C 15-D 27.

DESCRIPTION. This spathognathodid is characterized by having an oral outline that is straight in the mid-third, but which plunges steeply towards the posterior end. It has relatively few denticles on the oral edge and a widely flared, arched, basal cavity on the outer lateral face. The posterior end is shallow and pointed.

This short spathognathodid has a prominent plough-like antero-aboral area which may sometimes develop an irregular anterior edge. The antero-aboral margin is acute and more or less pointed and its posterior edge is feebly convex. The anterior edge of the unit is generally straight. The oral edge bears 9 denticles, which stand more or less erect to the general line of the blade, only their apices being discrete.

The denticles decrease regularly in size towards the posterior end of the unit, the posterior 2 or 3 tending to be minute in size. The anterior denticle is much the largest, but the subsequent 4 or 5 denticles tend to be of rather uniform size, and the mid-third of the unit has a rather straight lateral edge. In outer lateral view, the sharp flexure of the unit and the widely flared basal cavity are prominent features. The posterior end of the unit is very shallow. The aboral edge is continuously concave and the posterior edge is bluntly pointed. The basal cavity itself is confined to the mid-third of the unit and it is flared only on the outer lateral side, the inner side being straight.

Spathognathodus scitulus subsp. nov. A

Plate 31, figs. 12a-c

MATERIAL. 3 specimens : X 390 (figured).

RANGE. Scotland DUN 78.

DESCRIPTION. A *Spathognathodus scitulus* with one or two inconspicuous accessory denticles developed on the anterior edge of the main denticle.

The present specimens agree with typical individuals of *S. scitulus* (e.g. those illustrated by Rexroad & Collinson 1963, and Clarke 1960) except that the "cusp" (the most anterior denticle of the blade) has two small confluent denticles on its anterior aboral edge, which are developed parallel to the anterior margin. The denticles posterior to the main denticle, the general form of the blade, and the general structure and asymmetry of the basal cavity are otherwise similar to those of *Spathognathodus scitulus* s.s.

Spathognathodus cf. *campbelli* Rexroad

Plate 8, figs. 1A-4C

1957 *Spathognathodus campbelli* Rexroad : 37, Pl. 3, figs. 13-15.1960 *Spathognathodus pusillus* Clarke : 20-21, Pl. 3, figs. 10, 11.1965 *Spathognathodus* cf. *campbelli* Rexroad ; Rexroad & Nicoll : 26, Pl. 1, fig. 6.

MATERIAL. 11 specimens : figured, X 450, X 451, X 452, X 435.

RANGE. North Crop CYD 6-3D 19.

DESCRIPTION. The most distinctive features of the present specimens are the deep and relatively short blade, which is almost as deep as the longest oral denticles ; the series of up to 20 laterally compressed denticles of which the largest occurs at about mid-length ; the marked flaring of the basal cavity, which is confined to the posterior half of the unit ; and the gentle posterior deflection in a vertical plane of the posterior half of the unit. In lateral view the oral margin is sharply denticulated, tending to be straight and rather sloping in the anterior half, and more or less convex in the posterior half. There are 17 to 20 denticles on the oral edge of the blade. These show a rough increase in size from the anterior denticle to the denticle at about mid-length of the blade, which is the largest of the whole blade and is feebly inclined posteriorly to the basal surface of the blade. The other denticles of the anterior part of the blade are more or less erect and are confluent for most of their length, although their apical portions are discrete and pointed. The denticles of the posterior part of the blade are all inclined posteriorly. They are discrete for a greater part of their length than those of the anterior part of the blade, and the degree of posterior inclination tends to increase towards the posterior end of the blade. Those in the posterior quarter of the blade tend to be the smallest. The posterior blade decreases in depth posteriorly and the posterior end is shallow and bluntly spatulate. It is also conspicuously depressed in a vertical plane towards the posterior end. The other striking feature in lateral view is the widely flaring and elongate basal cavity, the anterior end of which is aligned with the anterior edge of the largest denticle.

In aboral view the cavity has a strongly biconvex outline and is extended virtually to the posterior end of the blade. It is continued anteriorly to the anterior edge of the main denticle as a very inconspicuous and narrow slit.

REMARKS. The present specimens differ somewhat from those described by Rexroad in having a rather conspicuously developed denticle at about mid-length. In other respects the specimens are closely similar, especially in the general form of the basal cavity, which tends to be more rounded anteriorly than it is posteriorly, and to have its deepest point near the anterior end. The longitudinal line immediately above the level of the navel, which marks the thin basal edges of the unit, is well seen under certain conditions of lighting.

Spathognathodus cf. *cristulus* Youngquist & Miller

Plate 8, figs. 7A-8C, 12A-13B

1938 *Spathognathodus regularis* Branson & Mehl (*partim*) : 137, Pl. 34, fig. 2 only (*non* Pl. 34, figs. 1, 3, 10 = *S. regularis*).

MATERIAL. 387 specimens : figured, X 554-X 557.

RANGE. North Crop ZLA 2-ZLA 33, Avon Gorge Z 35-D 27.

DESCRIPTION. This species is a simple denticulate unit bearing a regular succession of denticles which decrease in height from anterior to posterior. The anterior denticle tends to be massive, taller and nearly twice as wide as the remainder ; the next two denticles in a posterior direction tend to be fairly narrow and fused ; the remainder have free chevron-shaped tips and are slightly larger.

In aboral view the cavity is large with some flaring of the lips ; it begins immediately posterior to the anterior denticle and runs to the posterior termination of the unit. The lips are arched anteriorly and the whole cavity is symmetrical.

REMARKS. This form agrees very closely with *S. cristulus* (Youngquist & Miller, 1949 : 621, Pl. 101, figs. 1-3), except that their specimens commonly have 10 smaller denticles, whereas the present forms have from 7 to 16 denticles. They agree exactly with a form included in *S. regularis* (Branson & Mehl 1938A), even to the number of denticles. Branson & Mehl, and Rexroad & Scott (1964 : 50) recognize forms with one major anterior denticle within the specific terms of *S. regularis*, but since our fauna contains specimens with only one major denticle, and no specimens with the two anterior denticles typical of the holotype of *S. regularis*, there are obviously two separate species involved. The present specimens are compared to *S. cristulus* because of their close resemblance, but they are stratigraphically younger and may be a separate, perhaps ancestral, species.

Spathognathodus cf. *cyrius* (Cooper)

Plate 7, figs. 12a-14c

1939 *Spathodus sulciferus* Branson & Mehl ; Cooper (*partim*) : Pl. 45, fig. 17, (*non* Pl. 45, fig. 18 = *S. crassidentatus*).

1939 *Spathodus cyrius* Cooper : 413, Pl. 45, fig. 25.

non 1943 *Spathognathodus cyrius* (Cooper) Cooper & Sloss : 175, Pl. 28, figs. 3, 4, 10, 12 (= *S. crassidentatus*).

1951 *Spathognathodus macer* Branson & Mehl ; Youngquist & Downs : 791, Pl. 111, figs. 1, 2.

MATERIAL. 19 specimens : figured, X 470, X 469, X 471.

RANGE. North Crop KL 2-ZLA 2, Avon Gorge Z 1-Z 13.

DESCRIPTION. This is a simple arched and bowed unit which is highest at the anterior end ; the anterior part consists of 3 high denticles with the medial one the largest. The rest of the unit is made up of lower denticles, the medial part consisting of denticles of equal height and the posterior part shallowing with progressively smaller denticles. In the medial part the denticles are very fine and fused, 2 denticles commonly having only one emergent oral extremity. The unit commonly bears, besides the large anterior denticles, 30 smaller denticles.

The cavity is situated medially and is relatively small and pear-shaped.

REMARKS. This species bears a marked resemblance to *S. crassidentatus* and was included in that species by Rexroad & Scott (1964), but the very different dentition serves to distinguish it. The medial and posterior oral parts commonly bear 30 denticles, as opposed to the 15 or so of *S. crassidentatus*. Between the anterior part of the cavity and the anterior high blade, this species has 7 to 8 denticles whereas *S. crassidentatus* has only 2 to 3. Cooper's holotype has a total of only 20 denticles, but is otherwise very similar to the present specimens. The present specimens also resemble those described by Cooper (1939, Pl. 45, fig. 17 only) as *Spathodus sulciferus* Branson & Mehl (fig. 18 of Cooper's Pl. 45 is probably *S. crassidentatus*) and those described as *S. macer* by Youngquist & Downs (1951, Pl. 111, figs. 1, 2). *S. chou-teauensis* Cooper (1939, Pl. 45, fig. 20) is also broadly similar and also has resemblances to *S. crassidentatus*.

Spathognathodus cf. *robustus* (Branson & Mehl)

Plate 7, figs. 6a-7c

1934 *Spathodus robustus* Branson & Mehl : 189, Pl. 17, fig. 21.

MATERIAL. 17 specimens : figured, X 387, X 388.

RANGE. North Crop KL 19-ZLA 14, Avon Gorge K₂ 1.

DESCRIPTION. The unit is bar-like, being highest at the anterior end and sloping towards the posterior end, the oral outline being nearly straight. The anterior denticles tend to be massive. Smaller denticles appear on the anterior edge of the anteriormost massive denticle, giving a posteriorly inclined anterior edge which makes a sharp angle of about 60°, with the aboral edge. The denticles in the median part of the unit are fused, two denticles often fusing into one free tip. The posterior bar-like part of the unit is shallow, twisted and depressed downwards, the denticles tending to be isolated and free standing and curved towards the inner side.

In aboral view the cavity is fairly large, elongate, medially situated, about twice as long as wide, the wider anterior end narrowing rapidly towards the anterior of the unit and the other end narrowing slowly towards the posterior; the lips are thickened slightly.

REMARKS. Branson & Mehl (1934, Pl. 17, fig. 21) described a form very similar to ours as *S. robustus*. The dentition is very similar, except that in their specimen the massive anterior denticle and the isolated posterior denticles are less conspicuously developed than those of the present specimens.

There appears to be a morphological trend from these specimens through such forms as *Spathognathodus* sp. B. to a pseudopolygnathid form.

The *Spathognathodus tridentatus* group

Much confusion has arisen in recent conodont literature (Sannemann 1955, Bischoff & Ziegler 1956, Freyer 1961 and Ziegler 1962) with regard to specimens of the genus *Spathognathodus* which develop lateral denticles. *Spathognathodids* with

lateral denticles have been described by Branson & Mehl (1933), E. R. Branson (1934) and Scott (1961), from the Grassy Creek, Bushberg/Hannibal, and Louisiana Limestone Formations respectively.

German workers recognized a progressive addition of denticles, firstly on the inner lateral face, and secondly on the outer lateral face. Forms with denticles confined to the inner supra-cavity position were referred to *S. aculeatus* (Branson & Mehl), whereas forms with a development of lateral denticles along the whole length of the unit, except for the high anterior blade, were referred to subspecies of *S. costatus* (E. R. Branson). Scott (1962 : 1224) separated as a distinct species (*S. anteposicornis*), forms with a single node immediately anterior to the oral surface of the cavity.

From studies of the present British conodont faunas it appears that within the period Upper Devonian (to V) to Lower Carboniferous (Cu II α), there has been multiple development of laterally nodose spathognathodids. It appears that the Grassy Creek (to V) form *S. aculeatus* (Branson & Mehl) was the first species exhibiting this trend. No other to V forms with further development of lateral denticles on both lateral faces are known. Forms described from Germany and identified as *S. aculeatus* by Ziegler (1961) and other authors may be distinct from *S. aculeatus* and are probably a new species.

The further developments of this species referred by Ziegler to *S. costatus costatus*, *S. costatus spinulicostatus* and *S. costatus ultimus* are definitely not representative of the species *S. costatus* (E. R. Branson) and *S. spinulicostatus* (E. R. Branson), and are named herein as new species, *S. bischoffi* sp. nov. and *S. ziegleri* sp. nov.

S. costatus costatus (E. R. Branson) (= *S. costatus* of Branson) and *S. costatus sulciferus* (Branson & Mehl) (= *S. spinulicostatus* of E. R. Branson) appear to be restricted to an upper Cu I-Lower Cu II α range, and can be seen to develop into forms referable to the genus *Pseudopolygnathus*. The fact that species of this genus are found at lower horizons (e.g. the Devonian-Carboniferous boundary) indicates that the genus *Pseudopolygnathus* is polyphyletic, the ancestral forms in both cases probably being nodose spathognathodids, as suggested by Voges (1959).

Forms with from 2 to 4 lateral denticles, occurring with *S. costatus* (*sensu* E. R. Branson) and *S. spinulicostatus* (*sensu* E. R. Branson), appear referable to *S. tridentatus* (E. R. Branson), as distinct from *S. tridentatus* (*sensu* Sannemann, Bischoff & Ziegler and Freyer), the latter forms being better referred to *S. aculeatus* (*sensu* Ziegler).

In addition to these forms, there occurs at the base of the Lower Carboniferous in our sections, beneath and with the first occurrence of the genus *Siphonodella*, a new species of laterally denticulate *Spathognathodus*, with a plume-like anterior blade. Ziegler (1960A) described as *S. tridentatus* a form which appears referable to our new species *S. plumulus plumulus*. This species also exhibits evolutionary addition of denticles on the outer lateral cup but, rather than evolving to give species of the genus *Pseudopolygnathus*, it alters by lateral shift of the anterior blade into a homoeomorphic form of the genus *Cavusgnathus*, named herein as a new genus *Clydagnathus* (p. 85).

Spathognathodus tridentatus (E. R. Branson)

Plate 3, figs. 9a-12c

- 1934 *Spathodus sulciferus* Branson & Mehl; E. R. Branson : 304, Pl. 27, fig. 15 ? 22
(non Pl. 27, fig. 20 = *S. costatus sulciferus*).
- 1934 *Spathodus tridentatus* E. R. Branson : 307, Pl. 27, fig. 25.
- 1934 *Spathodus duplidens* Huddle : 91, Pl. 12, figs. 1-4.
- 1949 *Spathognathodus costatus* (E. R. Branson) Thomas : 409, 412, Pl. 4, fig. 10.
- 1949 *Spathognathodus tridentatus* (E. R. Branson) Thomas : 412, Pl. 4, fig. 11.
- non 1955 *Spathognathodus tridentatus* (E. R. Branson) Sannemann : Pl. 24, fig. 13.
- non 1956 *Spathognathodus tridentatus* (E. R. Branson) Bischoff & Ziegler : p. 167, Pl. 13,
figs. 1, 2.
- ? 1956 *Spathognathodus aciedentatus* (E. R. Branson) Hass Pl. 2, fig. 26.
- ? 1957 *Spathognathodus aciedentatus* (E. R. Branson) Cloud, Barnes & Hass : Pl. 5,
fig. 7.
- ? 1959 *Spathognathodus aciedentatus* (E. R. Branson) Hass : Pl. 49, fig. 24.
- non 1959 *Spathognathodus tridentatus* (E. R. Branson) Voges : 658, Pl. 3, fig. 7.
- non 1960 *Spathognathodus tridentatus* (E. R. Branson) Dvorak & Freyer : Pl. 2, figs. 9, 10.
- non 1961 *Spathognathodus tridentatus* (E. R. Branson) Freyer : 89, Pl. 6, fig. 150.
- non 1961 *Spathognathodus tridentatus* (E. R. Branson) Remack-Petitot : 261, fig. 4.

MATERIAL. 259 specimens : figured, X 394, X 395, X 396, X 397.

RANGE. North Crop KL 19-ZLA 27, Avon Gorge K 21-Z 24.

DESCRIPTION. The unit is straight to gently arched in the posterior part and slightly bowed ; it is highest at the anterior. The anterior blade is composed of 3 to 4 high denticles, the highest being the anterior-most 2 or 3 denticles. The median denticles are of equal height, and the unit shallows posteriorly, the denticles becoming shorter, less fused, and rather sharper towards the posterior end.

On the inner side there are developed from 2 to 4 lateral denticles, situated above the cavity. They are peg-like and are not connected to the main blade by transverse ridges.

In aboral view the basal cavity is large and symmetrically expanded, the widest part being at or just anterior to the mid-point. The cavity extends in either direction as a short aboral groove, the posterior groove being longer than the anterior.

REMARKS. This is a very common species with a limited range in our faunas. It is closely related to and occupies an intermediate phylogenetic position between *S. anteposicornis* and *S. costatus costatus*. It is also very close to *S. aculeatus*, but its higher stratigraphical position implies a distinct phylogenetic origin. For this reason it seems undesirable to regard it as a junior synonym of that species. The similarity between the two forms is, in any case, not exact. *S. aculeatus* has a more conspicuously laterally expanded basal cavity. Individuals from stratigraphically older samples (e.g. Pl. 3, figs. 11a-c) tend to have a smaller number of blade denticles (9 to 13) behind the anterior blade than those from younger samples (e.g. Pl. 3, figs. 10a-c), which have from 14 to 19 denticles.

Spathognathodus ziegleri sp. nov.

Plate 4, figs. 5a-8d

- non 1934 *Spathodus spinulicostatus* E. R. Branson : 305, Pl. 27, fig. 19 [= *S. sulciferus*].
 1956 *Spathognathodus spinulicostatus* (E. R. Branson) Bischoff & Ziegler : 167, Pl. 13, fig. 7.
 1957 *Spathognathodus spinulicostatus spinulicostatus* (E. R. Branson) Bischoff : 57, pl. 4, fig. 27.
 1957 *Spathognathodus spinulicostatus spinulicostatus* (E. R. Branson) Ziegler in Flügel & Ziegler : Pl. 1, fig. 14.
 1959 *Spathognathodus spinulicostatus spinulicostatus* (E. R. Branson) Helms : Pl. 3, figs. 12a, b.
 1960 *Spathognathodus spinulicostatus spinulicostatus* (E. R. Branson) Remack-Petitot : 261, fig. 4.
 1960 *Spathognathodus spinulicostatus spinulicostatus* (E. R. Branson) Dvorak & Freyer : Pl. 2, fig. 8.
 1961 *Spathognathodus spinulicostatus spinulicostatus* (E. R. Branson) Freyer : 87, 88, Pl. 6, fig. 145, text-fig. 146.
 1962 *Spathognathodus costatus spinulicostatus* (E. R. Branson) Ziegler : 108, Pl. 14, figs. 11-18.
 1965 *Spathognathodus spinulicostatus spinulicostatus* (E. R. Branson) Spasov : 102, Pl. 3, figs. 13, 17.

DERIVATION OF NAME. This is named in honour of Dr. W. Ziegler.

DIAGNOSIS. *Spathognathodus* with subdued oral denticulation. Anterior blade deep, but narrowing posteriorly, oral surface being flat. Strong development of accessory lateral denticles, up to 13 in number, on outer side of unit. On opposite side, posterior end of unit also marked by development of up to 7 smaller lateral denticles, giving whole posterior part an asymmetrical platform-like development. Basal cavity strongly laterally expanded, but lanceolate in basal outline.

MATERIAL. Holotype X 403, Paratypes X 402, X 404, X 437 (all figured).

TYPE LOCALITY AND HORIZON AND RANGE. Hönnetal, West Germany to VI Zone—Upper *costatus* Zone, roadside cutting (Ziegler 1962).

DESCRIPTION. In lateral view the anterior blade is deep but straight, the oral surface bearing a series of reduced even denticles, only the anterior 3 or 4 of which have sharply defined apices. There is a tendency for the depth of the anterior blade to decrease towards the basal cavity, but the oral edge is straight. Behind the basal cavity there is a marked reduction in depth of the unit as seen in lateral view. The aboral edge remains more or less straight, but the oral surface slopes down to meet it in a relatively straight line. Its oral edge makes an angle of about 160° with the oral edge of the blade. The posterior end is spatulate to bluntly-pointed in lateral view. The basal cavity is a conspicuous feature when seen in lateral view. The oral posterior surface of the unit bears a series of low irregular denticles developed lateral to the main blade, but clearly visible in lateral view. These denticles, are developed on the inner lateral face of the unit. In outer lateral view the unit is broadly similiar.

In oral view the most striking feature of the unit is the development of up to 13

laterally expanded denticles developed on the outer (convex) side of the main blade. These are barely visible in lateral view, but are conspicuously elongated blunt denticles in oral view. On the inner (concave) side posterior to the basal cavity, there is a series of up to 7 broadly similar denticles developed. The two sets of denticles tend to form a more or less continuous ridge across the posterior platform which they produce, although in some specimens they are arranged at such an angle to one another to give an arrow-like oral view. The basal cavity is conspicuously laterally expanded in oral view, the inner end of its long axis, which lies oblique to the main axis of the unit, lying anterior to that of the outer side.

In aboral view the cavity is laterally expanded, the greatest width lying near its anterior end. It is shallow and asymmetrical and tapers more or less uniformly towards the posterior termination of the unit, having an overall lanceolate lachryform outline, the anterior end being rounded.

REMARKS. This species differs from *S. bischoffi* in the development of an accessory row of posterior lateral denticles. Like that species, no mirror images of forms are known. In this the two species resemble many species of the genus *Pseudopolygnathus*, to which both are closely related in their overall morphology.

Spathognathodus sp. A

Plate 4, figs. 12a-c

MATERIAL. 4 specimens : figured, X 405.

RANGE. North Crop KL 3-KL 5.

DESCRIPTION. The unit is arched, relatively short and deep. The major denticles or pair of denticles occur in the anterior quarter, being massive, tall, and laterally compressed. The anterior blade occurs anterior to this denticle and is formed of denticles developed in a fan-like manner on both the oral and anterior faces of the unit. The median part of the blade is fairly level, but the posterior part decreases in



FIG. 47. The development of *Pseudopolygnathus postinodosus* from a spathognathodid ancestor by addition of lateral denticles.

height rapidly near the posterior termination. The aboral outline of the unit is arched, the basal cavity being elongate and without flared lips.

REMARKS. This species appears to be dissimilar to all other described species of spathognathodids, although it is closest to *S. crassidentatus*.

Spathognathodus sp. B

Plate 7, figs. 8a-c

MATERIAL. 4 specimens : figured, X 406.

RANGE. North Crop ZLA 5, Avon Gorge Z 34-C 7.

DESCRIPTION. The bar is fairly massive being highest anteriorly, with the height decreasing regularly to the posterior ; the posterior termination is broken. The anterior-aboral portion of the blade is extended anteriorly as a short flattened process. The denticles, at least 17 in number, are laterally compressed and fused over the majority of their length. One lateral denticle occurs immediately anterior to the anterior margin of the cavity, and reaches the height of the main blade denticles. The aboral profile of the unit is not straight, the cavity tending to arch the posterior part upward.

In aboral view the cavity is elongate and moderately flared, extending as a groove for a short distance posteriorly and anteriorly.

REMARKS. This form is probably a pathological variant of *S. cf. robustus*, the lateral dentition placing it in an intermediate position between this and *Pseudopolygnathus* sp.

Spathognathodus sp. nov.

Plate 6, fig. 9

MATERIAL. 15 specimens : figured, X 518.

LOCALITY AND HORIZON. Avon Gorge. Sample Z 19.

RANGE. Avon Gorge Z 13-Z 19.

DESCRIPTION. A spathognathodid characterized by finely developed oral denticulation on a bar which is deep and protruding antero-aborally, becoming shallower towards its posterior end. The bar is strongly recurved in its posterior half. The basal cavity is strongly expanded laterally, and one or more lateral denticles are developed on the oral edge. The whole unit tends to be gently curved in a horizontal plane, and is clearly transitional towards a pseudopolygnathid condition.

The basal bar is deepest anteriorly, and the anterior edge and antero-aboral margin make an angle of about 70° with one another, so that the antero-aboral angle protrudes strongly when seen in lateral view. The basal bar decreases in depth posteriorly. The anterior third has a straight aboral margin, but the posterior two thirds tend to be gently but continuously arched. The posterior end is bluntly spatulate. The oral surface bears a series of closely spaced acicular denticles, of which only the apices tend to be discrete. They are long, slender, and subequal

in length. Single accessory lateral denticles are developed in the anterior half on each side of the blade.

The basal cavity is situated slightly posterior to the mid-point of the unit. It is very strongly flared laterally and shows a clear tendency to a pseudopolygnathid development, but the cavity itself, in spite of its wide flaring lips, tends to be small. It extends anteriorly and posteriorly as a shallow groove. The whole unit is gently bowed inwards in a horizontal plane.

Genus *TAPHROGNATHUS* Branson & Mehl

1941 *Taphrognathus* Branson & Mehl : 181 (*non* Welles 1947).

TYPE SPECIES. *Taphrognathus varians* Branson & Mehl.

Taphrognathus varians Branson & Mehl

Plate 13, figs. 4a-5d

1940 *Taphrognathus varians* Branson & Mehl : 182, Pl. 6, figs. 27-33, 35-40.

1944 *Taphrognathus varians* Branson & Mehl ; Branson & Mehl : 246, Pl. 94, figs. 66-68.

1947 *Taphrognathus varians* Branson & Mehl ; Cooper : 92, Pl. 20, figs. 14-16.

1963 *Taphrognathus varians* Branson & Mehl ; Rexroad & Collinson : 21, Pl. 1, figs. 18-20, 22.

1965 *Taphrognathus varians* Branson & Mehl ; Rexroad & Collinson : 24, Pl. 1, figs. 30-32.

MATERIAL. 11 specimens : figured, X 408, X 407.

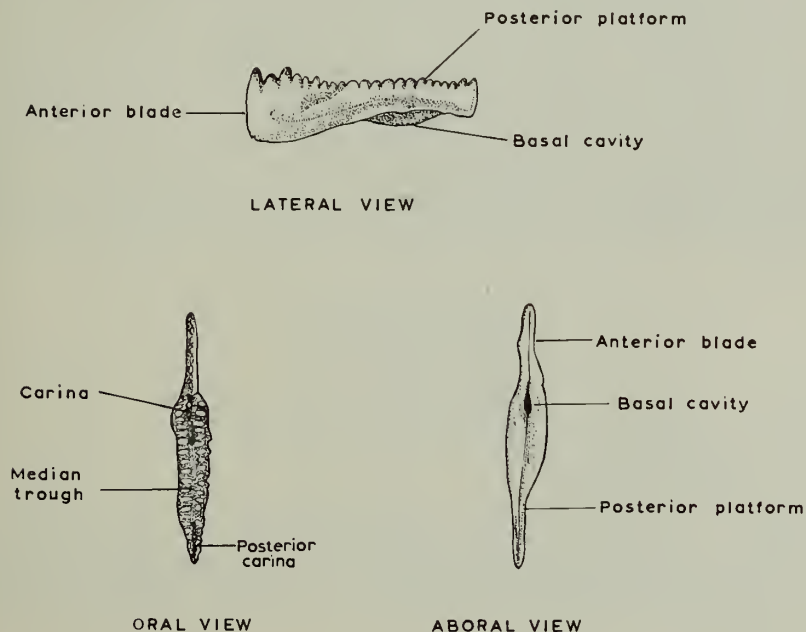


FIG. 48. *Taphrognathus* sp. showing morphological terms used in the text.

RANGE. Avon Gorge S 45-S 58.

DESCRIPTION. The distinctive feature of this species is its general elongate form and its median anterior blade. This is continued posteriorly for a short distance on the platform as a short carina. The median trough is narrow but deep, and the whole platform is conspicuously lanceolate in oral view, with straight or only gently convex lateral margins and a conspicuously pointed posterior end. The posterior median part of the platform bears a nodose to sharp, short carina, which extends only a short distance onto the platform beyond the posterior end, but is also extended posteriorly beyond the termination of the platform proper. The blade tends to be rather long, with fused denticles. The platform is smooth and V-shaped, and relatively deep in relation to its width. It has regularly and bluntly crenulate lateral margins and the whole platform tends to decrease in width aborally, so that the aboral edge at the posterior end is more or less sharp. There is an elongated aboral cavity below the anterior third of the platform which is shallow and flaring and more or less symmetrical. It is extended anteriorly and posteriorly as a thin, slit-like excavation.

The anterior blade is deeper than the adjacent part of the posterior platform and the denticles are bluntly tipped and coalesced.

The present specimens show some variation in the degree of posterior constriction, in the development of the posterior carina, and in the form of denticulation of the anterior bar.

REMARKS. Rexroad & Collinson (1963 : 20) have shown that the genus *Taphrognathus* and the genus *Cavusgnathus* are closely related and that in some faunas transitional forms between these two genera can be seen. In our faunas transitional forms are also found (Pl. 13, figs. 1-3c). The medial blade of *Taphrognathus* appears to move to take up an outer lateral position. However, since the blade is not completely lateral, it is difficult to determine whether these specimens belong to the genus *Taphrognathus* or to the genus *Cavusgnathus*. We have followed Rexroad & Collinson in placing them as transitional species between the two genera. They can be seen to be transitional, not only in the form of the anterior blade, but also in the general outline of the cavity, and in the reduction of the posterior carina.

Gen. nov. A sp.

Plate 25, figs. 6a, b

MATERIAL. 1 specimen : figured, X 409.

LOCALITY AND HORIZON. North Crop. Sample ZLA 6.

RANGE. North Crop ZLA 6.

DESCRIPTION. The unit is of a hibbardellid type, but the anterior arch is separated from the apical denticle by a short, denticulate, anterior bar. The anterior arch is broken, but can be seen to be denticulate. The apical denticle is massive, sub-circular in cross-section and is curved posteriorly. The posterior bar is thin and finely denticulate.

In aboral view the unit is excavated, the basal cavity running from the apical

C
Z
K

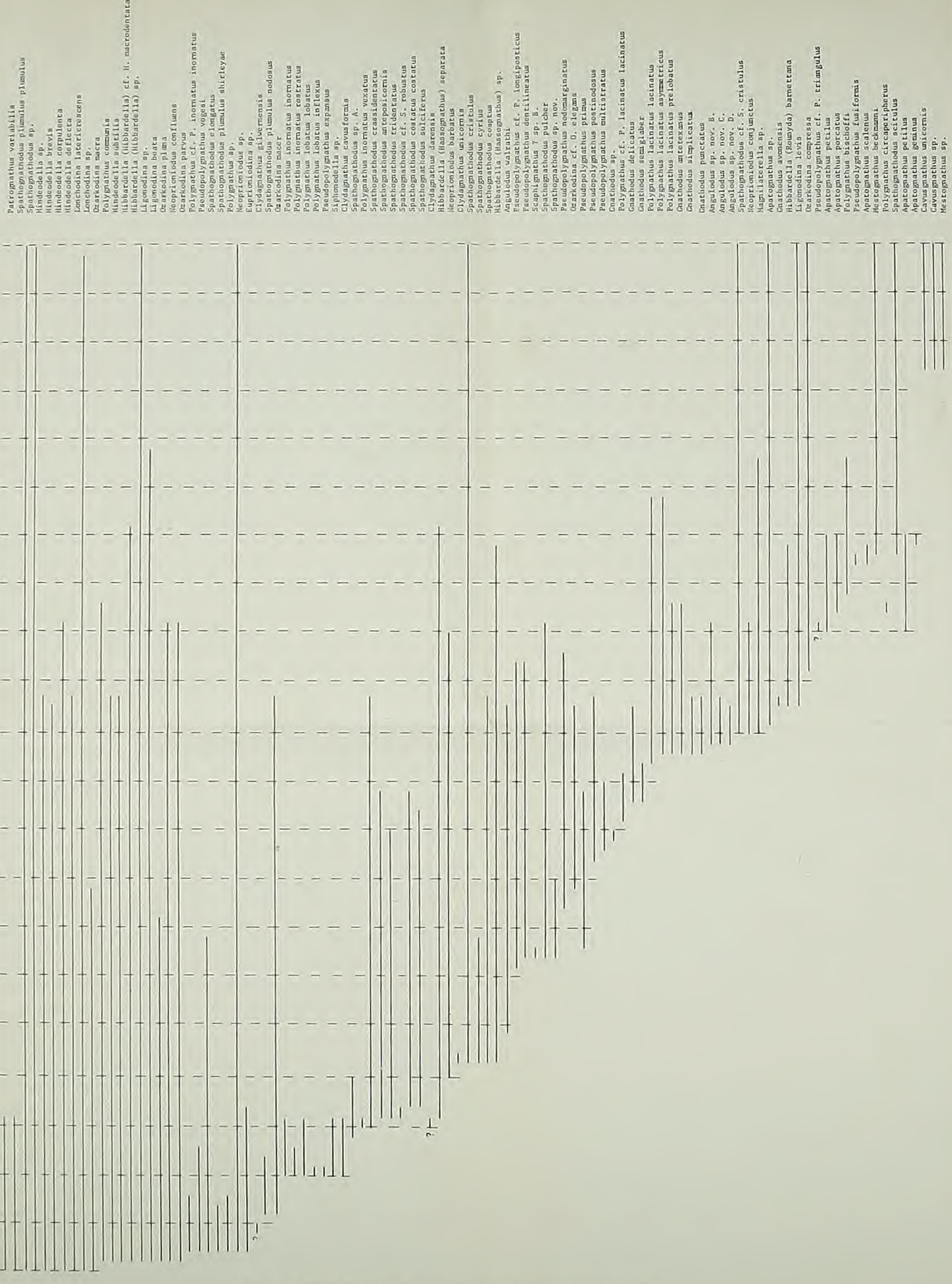


Fig. 49. Chart to show ranges of species in the C, Z and K Zones of the Avon Gorge.

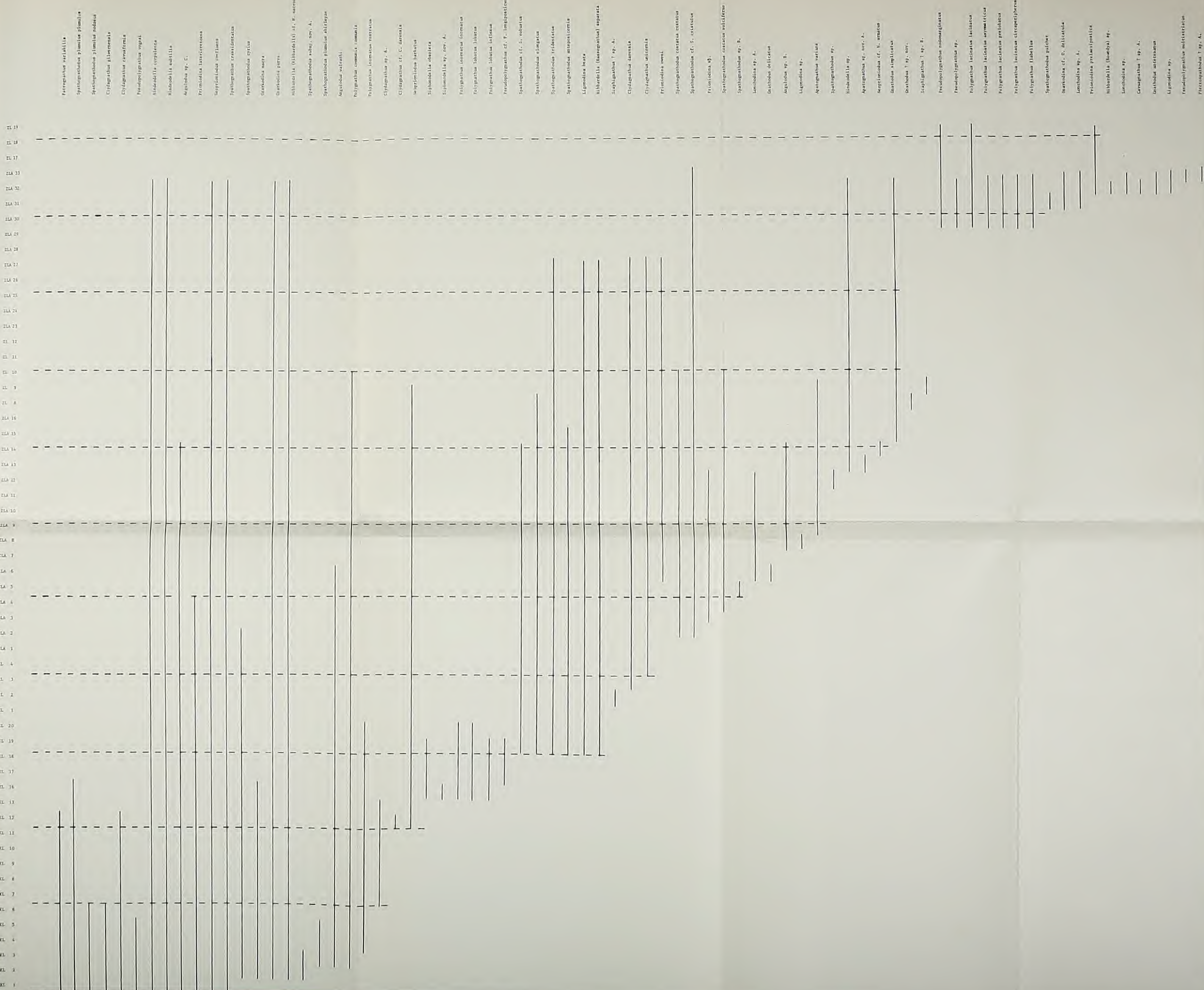
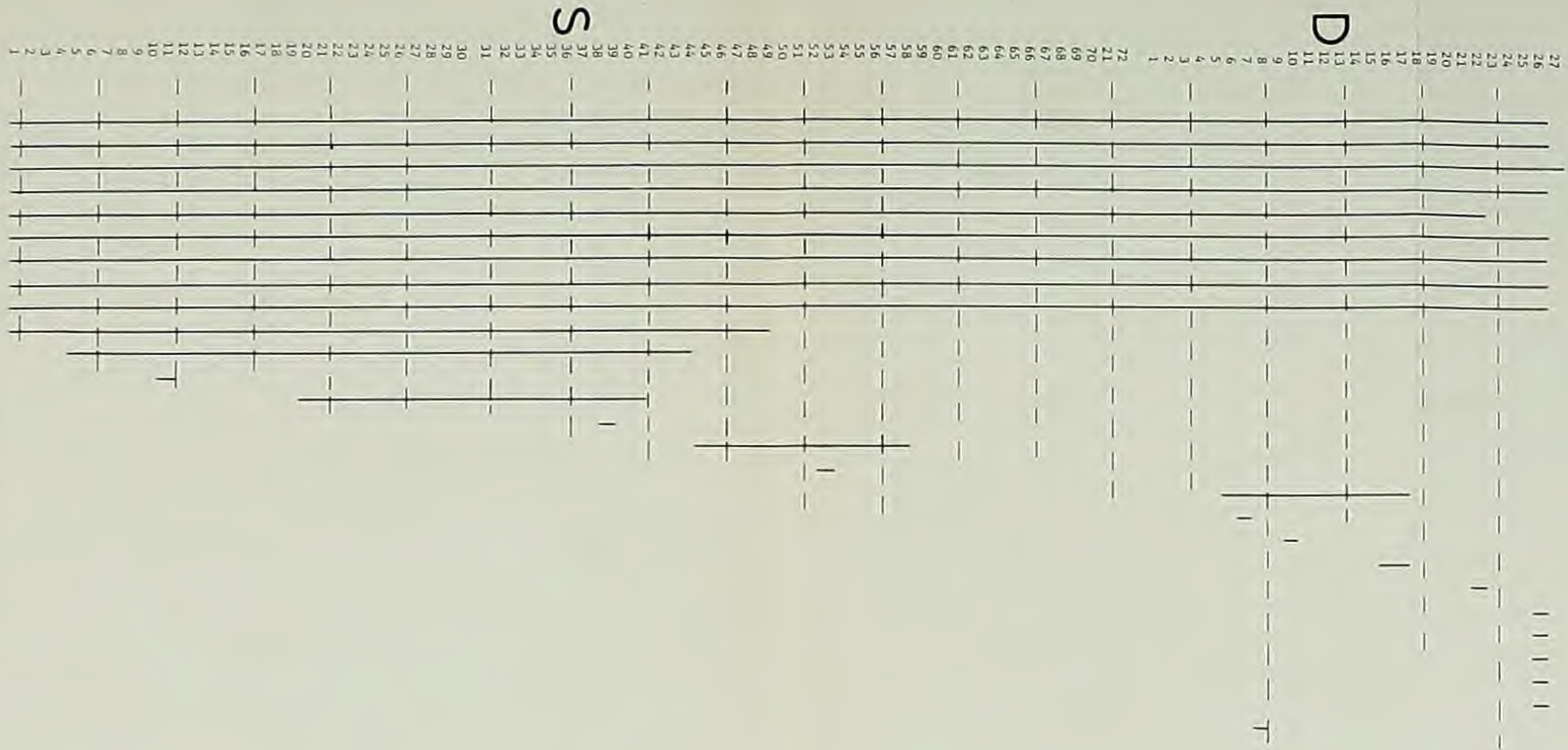


Fig. 50. Chart to show the ranges of species in the Z and K Zones of the North Crop, Samples KL 1-20, K Zone; ZL 1-19, Z Zone.



- Spathognathodus acitulus*
- Spathognathodus cristulus*
- Spathognathodus cf. S. cristulus*
- Spathognathodus sp.*
- Apatognathus sp.*
- Hindeodella sp.*
- Neoprioniodus sp.*
- Ligonodina sp.*
- Ligonodina levis*
- Ozarkodina compressa*
- Cavusgnathus characterus*
- Gnathodus cuneiformis*
- Cavusgnathus convexus*
- Apatognathus libratus*
- Taphrognathus varians*
- Gnathodus commutatus*
- Mestognathus neddensis*
- Apatognathus chauliodus*
- Gnathodus punctatus - G. bilineatus*
- Mestognathus bipluci*
- Polygnathus sp.*
- Cavusgnathus cristulus*
- Cavusgnathus naviculus*
- Gnathodus girtyi girtyi*
- Gnathodus girtyi simplex*
- Apatognathus cf. A. petilus*
- Apatognathus petilus*

Fig. 51. Chart to show the ranges of species in the D and S Zones of the Avon Gorge.

3D 22
 3D 21
 3D 20
 3D 19
 3D 18
 3D 17
 3D 16
 3D 14/15
 3D 13
 3D 12
 3D 11
 3D 10
 3D 9
 3D 8
 3D 7
 3D 6
 3D 5
 3D 4
 3D 3
 3D 2
 3D 1
 CYD 7
 CYD 6

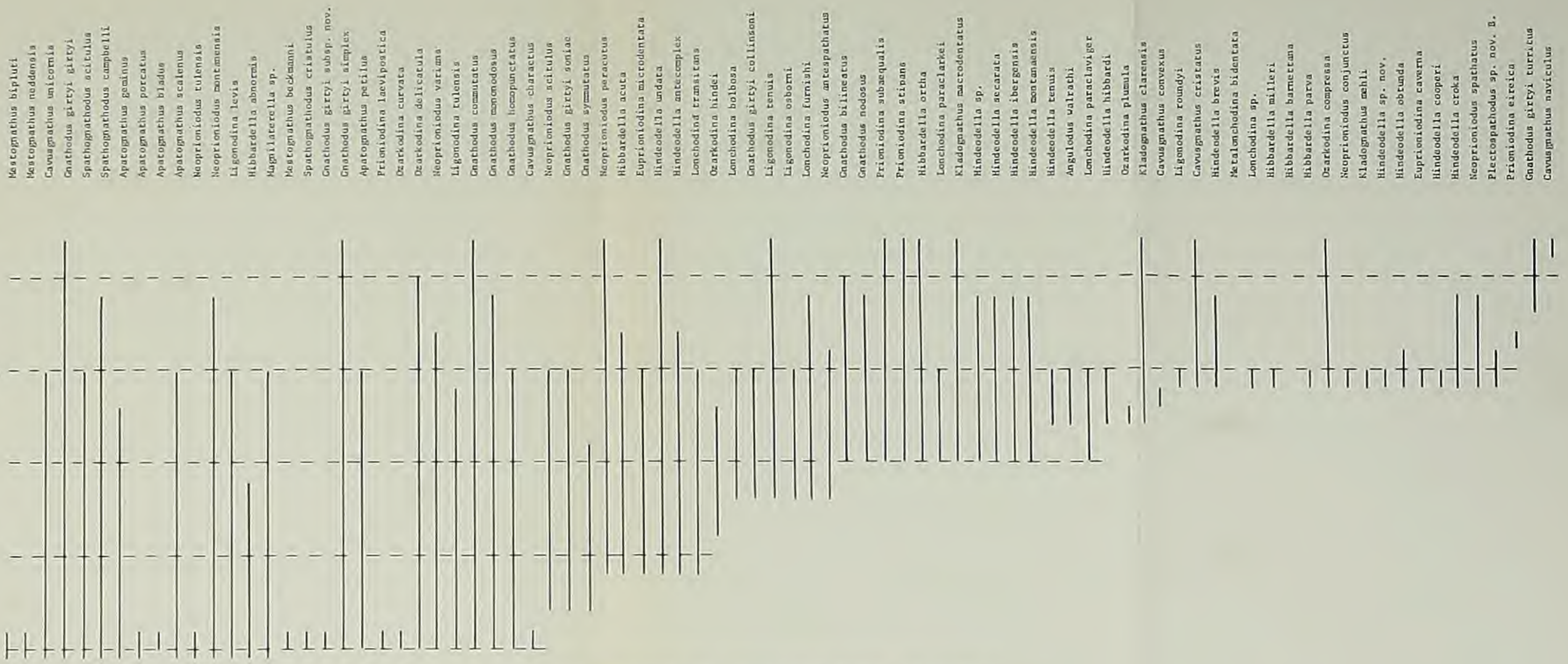


FIG. 52. Chart to show the ranges of species in the D₃ Subzone of the North Crop.

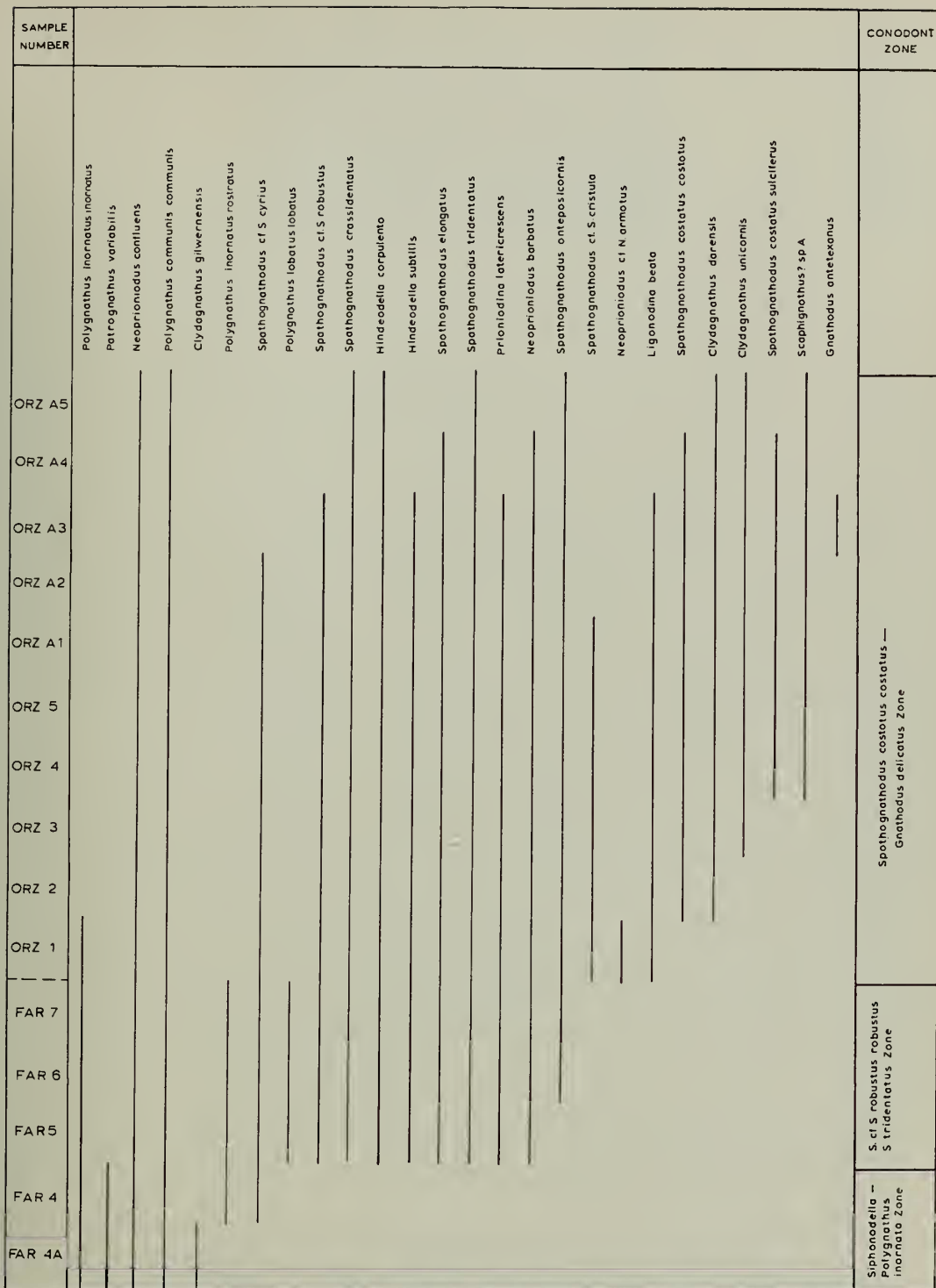


FIG. 53. Chart to show the ranges of species at Farlow. Samples FAR 4-7, K Zone : ORZ 1-A5, Z Zone.

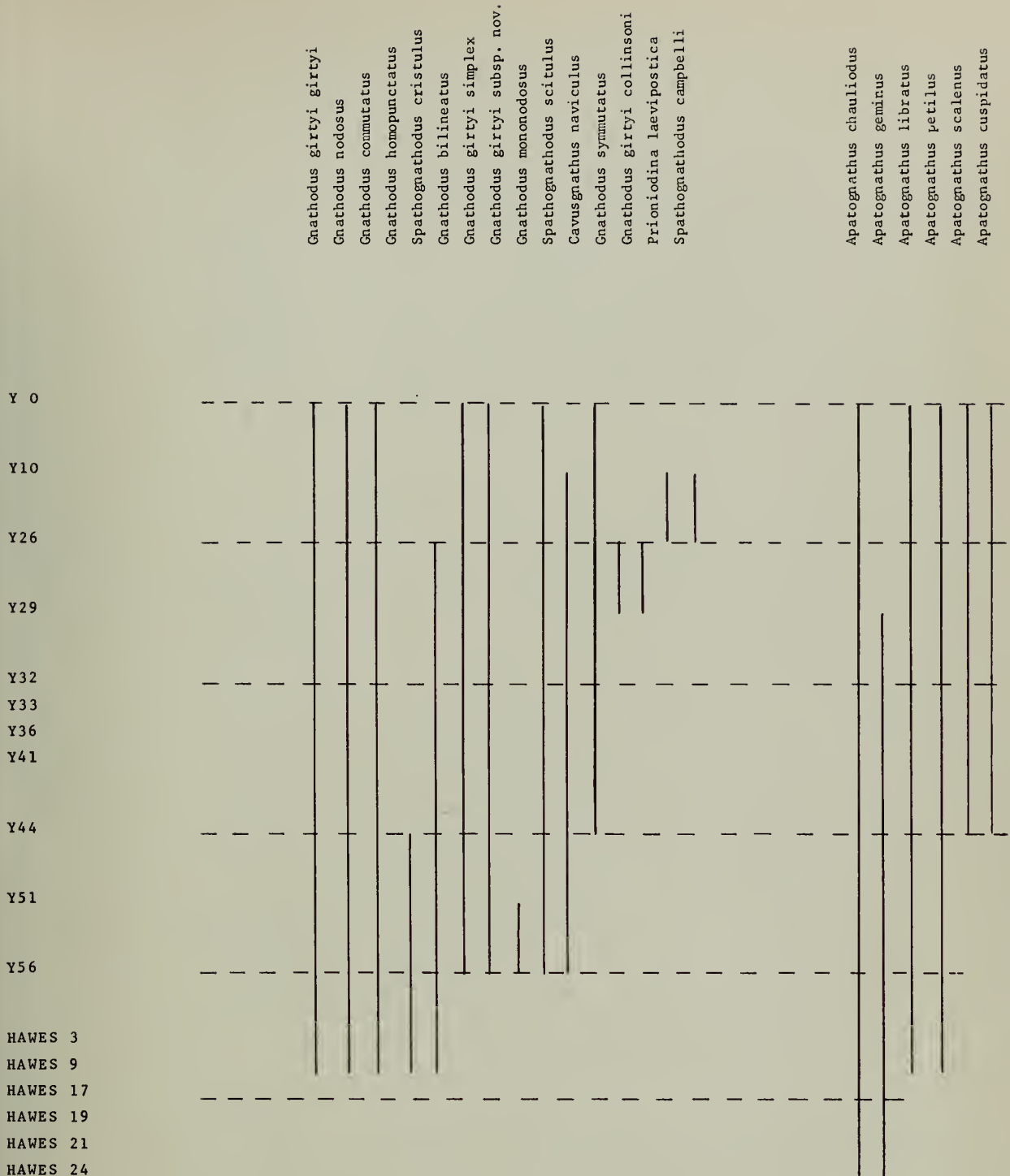


FIG. 54. Chart to show the range of selected conodont species in the Yoredale succession. Apatognathid species are shown separately. Samples Hawes 24, *Girvanella* Bed : Hawes 21, Hawes Limestone : Hawes 17, Gayle Limestone : Y 56 Hardraw Scar Limestone : Y 50 Limestone IIIA : Y 44 Simonstone Limestone : Y 36, Limestone IVA : Y 33, Limestone IVB : Y 29, Middle Limestone : Y 26, Five Yard Limestone : Y 10, Three Yard Limestone : UND 1, Underset Limestone.

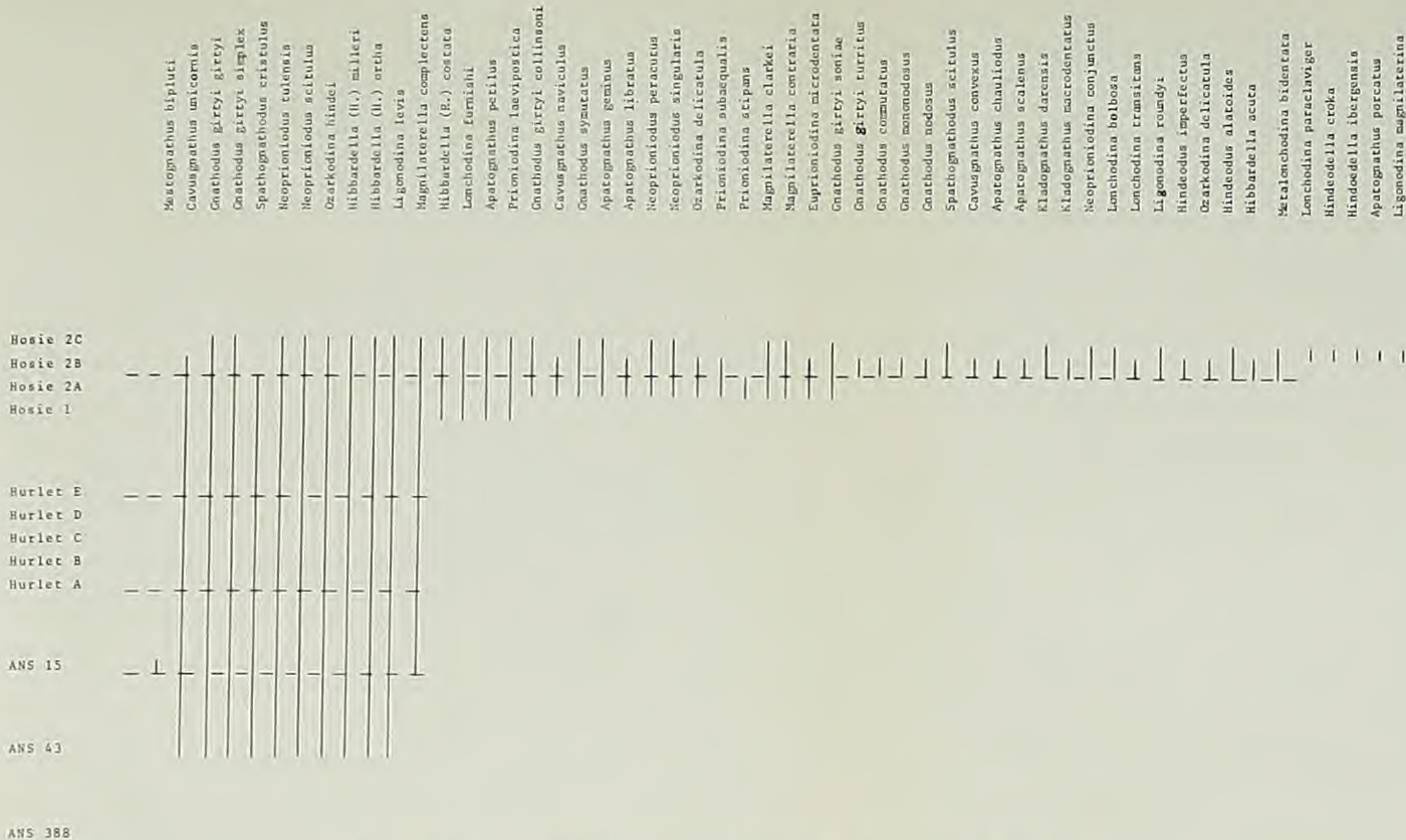


FIG. 55. Chart to show the ranges of conodont species in the Fife succession. Samples ANS 388-15, Calciferous Sandstone Series : Hurler, Hurler Limestone : Hosie, Hosie Limestones.

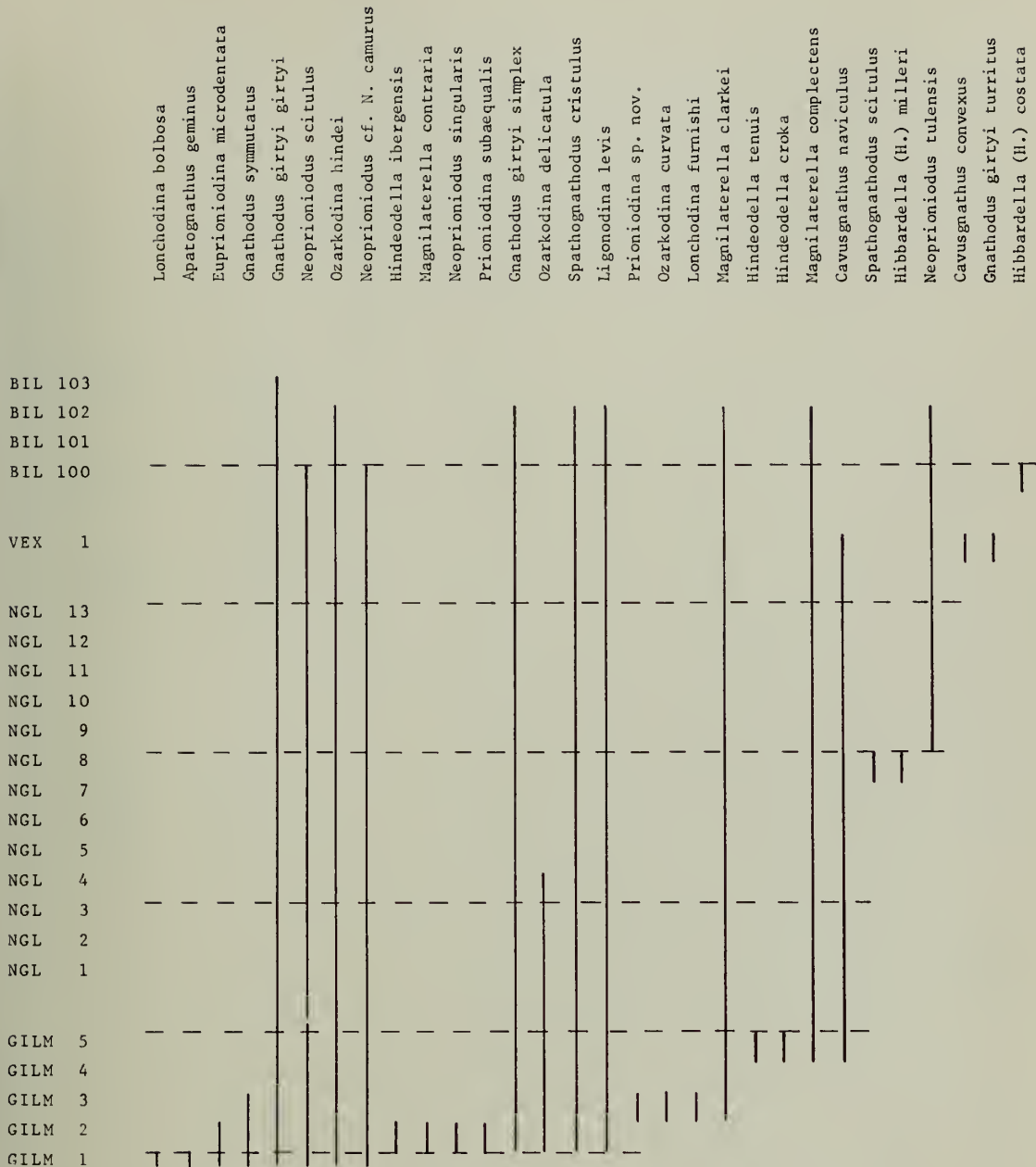


FIG. 56. Chart to show the ranges of conodont species in the Midlothian succession. Samples GILM, "Gilmerton Limestone": NGL, North Greens Limestone: VEX, Lower Vexhim Limestone: BIL, Bilston Burn Limestone.

- Gnathodus bilineatus
- Gnathodus girtyi girtyi
- Gnathodus girtyi simplex
- Gnathodus monodosus
- Spathognathodus cristulus
- Ligonodina levis
- Neoprioniodus scitulus
- Neoprioniodus peracutus
- Hibbardella milleri
- Magnilaterella clarkei
- Magnilaterella contraria
- Magnilaterella complectens
- Ligonodina roundyi
- Gnathodus commutatus
- Metalonchodina bidentata
- Apatognathus petilus
- Ligonodina osborni
- Neoprioniodus tulensis
- Spathognathodus scitulus
- Gnathodus girtyi collinsoni
- Cavusgnathus unicornis
- Apatognathus geminus
- Neoprioniodus singularis
- Apatognathus porcatus
- Gnathodus symutatus
- Apatognathus scalinus
- Lonchodina furnishi
- Geniculatus claviger
- Neoprioniodus conjunctus
- Mestognathus bipluti
- Mestognathus neddensis
- Lonchodina paraclaviger
- Lonchodina transitans
- Apatognathus chauliodus
- Ligonodina magnilaterina
- Prioniodina laevipostica
- Lonchodina obtunda
- Cavusgnathus naviculus
- Neoprioniodus varians
- Ozarkodina hindei
- Gnathodus girtyi turritus
- Gen nov. A et sp. B.
- Gnathodus nodosus
- Apatognathus libratus
- Magnilaterella robusta
- Spathognathodus scitulus subsp. nov.
- Lonchodina bolbosa
- Lonchodina paraclarki
- Hibbardella (R.) costata
- Ozarkodina delicatula
- Prioniodina subaequalis

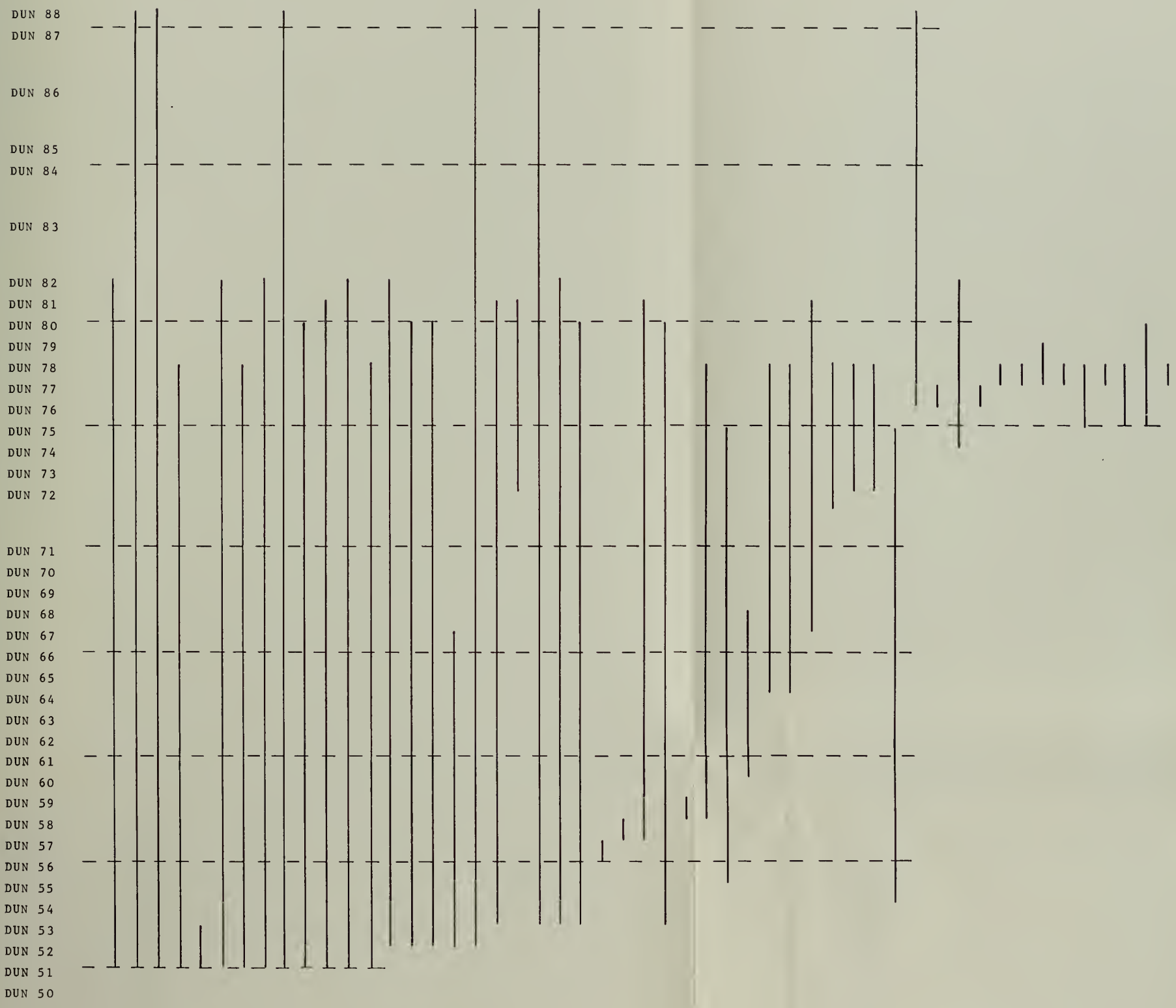


FIG. 57. Chart to show the ranges of conodont species in the Dunbar succession. Samples DUN 50-71, Long Craig Upper Limestone : DUN 72-82, Skateraw Limestones : DUN 84, 85, Chapel Point Limestone : DUN 86, Dryburn Foot Limestone : DUN 87, 88, Barnes East Limestone.

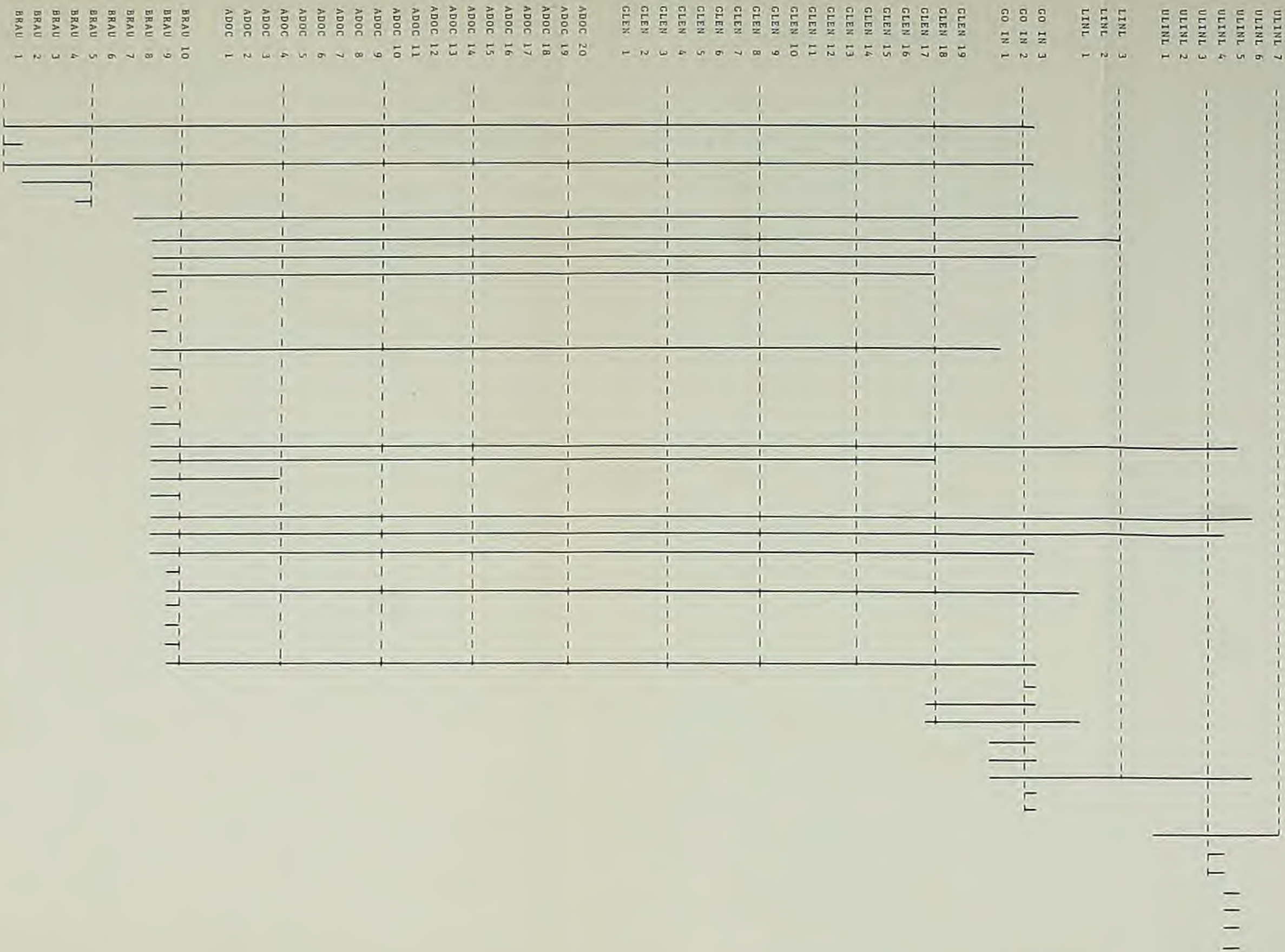


FIG. 58. Chart to show the ranges of conodont species in the Ayrshire succession. There was a general absence of conodonts in residues of 'high ADOC and low GLEN' samples, but ranges of persistent species are carried through this interval. Samples BRAU Broadstone Limestone; BRAU 9, 19, ADOC 1-20 Doctra Limestone; GLEN 1-19 Hose Limestone; GO IN 1-3 Index Limestone; LINL 1-3 Lower Linn Limestone; ULINL 1-7 Upper Linn Limestone.

denticle anteriorly to the anterior arch beneath the anterior bar, and posteriorly to where the posterior bar is broken.

REMARKS. This form is unlike any other described conodont genus.

Gen. nov. B. sp.

Plate 25, figs. 7a, b

MATERIAL. 1 specimen : figured, X 410.

RANGE. Farlow ORZ 1.

DESCRIPTION. This specimen is one of problematical affinities ; its essential features are that it has a conspicuous, elongated, main denticle, which is subtriangular in cross-section, with a more or less sharp anterior edge. Its anterior aboral margin is very flat, but has a narrow slit extending for a minute distance up the median part of the face. It is recurved posteriorly, even though there is no posterior bar. Its base is very thick-lipped and is regularly expanded as a relatively wide and deep cavity. It appears that this anterior denticle is complete, though this is not certain. On the outer lateral face, there is an anterior aboral process which makes an angle of about 90° with what would be the line of the posterior bar, and it is also depressed in a vertical plane. Its anterior face is very convex in anterior view, and its anterior distal end is straight-edged, with a sharp antero-aboral corner, but this is fractured in the specimen. Its oral surface bears 3 denticles, of which the two innermost are massive, with bluntly formed lateral edges and strongly convex anterior and posterior faces. The denticle at the distal end is conspicuously smaller than the other two, and the interior denticle, although very broad at the base, divides distally to give 2 separate denticles. There is a tendency for germ denticles to develop between the larger denticles. The posterior lateral face of the anterior aboral process is flat and the base is continuously excavated.

REMARKS. The fact that this specimen appears essentially complete makes it impossible to assign it to any existing genus. It may, in fact, represent a new one, but it is possible that it is a broken specimen of *Hindeodella corpulenta*.

VII. SUMMARY AND CONCLUSIONS

(a) *Scope of the present work*

During the last decade, studies in both Germany and the United States have demonstrated the potential value of conodonts in Carboniferous and Devonian stratigraphical correlation. The present study represents a comprehensive description of the conodont faunas of the British Lower Carboniferous, and a detailed analysis of their stratigraphical distribution. This has been used to erect a zonal scheme, by means of which a more precise correlation has been established between sections in each of the main British Carboniferous depositional provinces than any yet available on the basis of other faunal groups. Intercontinental correlations are also suggested.

(b) *Previous research*

A critical review of previous research on Carboniferous conodont faunas is given, together with a review of the present status of Carboniferous stratigraphical correlation (p. 17).

(c) *Collecting localities*

Samples have been collected from each of five major depositional areas. This has provided an indication of the degree of variability of conodont faunas both within and between depositional basins. In all some 3½ tons of limestone has been processed.

Avon Gorge, Bristol

Detailed sampling of this area has involved the digestion of some 189 'major' rock samples, most of them about 10 lbs in weight. Every 10 ft. of the section was sampled, and these samples were supplemented in critical parts of the succession by others taken at 5 ft. and 2 ft. intervals. The stratigraphy of the collecting areas is described in detail (p. 18).

North Crop of the South Wales Coalfield

A series of eleven localities in Brecknockshire and Monmouthshire was used to construct a composite Lower Carboniferous section, and small collections were made from Gower and Pembrokeshire. The middle part of the Avonian succession is generally not fossiliferous in this area, but the higher parts of the *Dibunophyllum* Zone have been used to complement the zonal scheme for the lower part of the section, established in the Avon Gorge.

Shropshire

The thin development of the Z and K Zones at Farlow and Oreton have yielded well-preserved faunas (p. 25).

Yorkshire

Sampling of the Yoredale succession in the type area has provided material for a reconnaissance survey of Yoredale conodont faunas. They show close similarities to those of the higher zones from the South Western Province.

Scotland

Extensive collections have been made from Dunbar, Roxburgh, Midlothian, Fife, Ayrshire and Argyll. All the major limestones in the succession were sampled, some at intervals of six inches, and most yielded well-preserved faunas.

(d) *Methods of study*

Most of the 25,000 specimens which form the basis of the study were extracted by digestion of limestone in 8% acetic acid. Methods of preparation and photography are described. The abundance of conodonts in each sample has been recorded (Figs 59-92).

(e) *Stratigraphic ranges*

The precise ranges of all conodont species recovered are shown by range charts (Figs. 49–58). The ranges of the more stratigraphically useful genera and species are described. *Patrognathus* gen. nov. is confined to the K Zone. *Clydagnathus* gen. nov. is found in the K and Lower Z Zones of the North Crop and Shropshire, but is rare in large faunas of the same age from the Avon Gorge. *Siphonodella* is very rare in the Avonian, being confined to the Upper K Zone (p. 32).

Pseudopolygnathus extends from the basal K to the C₁ Zone. It is represented by numbers of short-lived species and is abundant in the Avon Gorge, but less common in the North Crop (p. 32).

Gnathodus is a long-ranging Avonian genus, but individual species are valuable for correlation in the Z, C and D Zones (p. 34). *Spathognathodus* is equally long-ranging, but several short-lived species are valuable index fossils in various portions of the succession.

Polygnathus ranges from the K to the top of the C₁ Zone, and is represented by a number of species. *Mestognathus* extends from the C₁ to the D₂ Zone (p. 35), while *Cavusgnathus* is most characteristic of the C₂, S and D Zones. *Taphrognathus* is restricted to the Upper S₂ Subzone (p. 35) in the south west, but occurs in the C Zone of Roxburghshire.

Fourteen conodont assemblage zones are established

(f) *Geographic variation*

Our study shows several striking examples of what appear to be geographical differences in contemporaneous conodont faunas. These include representatives of the genera *Siphonodella* (p. 32), *Pseudopolygnathus* (p. 32), and *Clydagnathus* (p. 32) among others. These differences reflect variation not only between faunas separated by intercontinental distances, but also between faunas from the same general depositional basin (e.g. the Avon Gorge and the North Crop). The degree of such geographic variation is shown to be often greater than that generally admitted by most conodont workers, and is an important consideration in stratigraphic correlation. The absence of certain conodont genera and species from some areas may represent either the absence of one or more groups of conodont-bearing animals (conodontifers) of whatever taxonomic level, or the homoeomorphic replacement of certain conodonts within the same broad type of natural assemblage of the conodontifers.

(g) *Correlation within the British Avonian*

Avon Gorge–North Crop

The broad equivalence of Vaughan's coral–brachiopod zones as recognized in these two areas is supported by a comparison of the conodont faunas. The basal K strata of the North Crop are probably slightly younger than those of the Avon Gorge. The Upper K Zone of the Avon Gorge is equivalent to the uppermost K and basal Z Zones of the North Crop (p. 46).

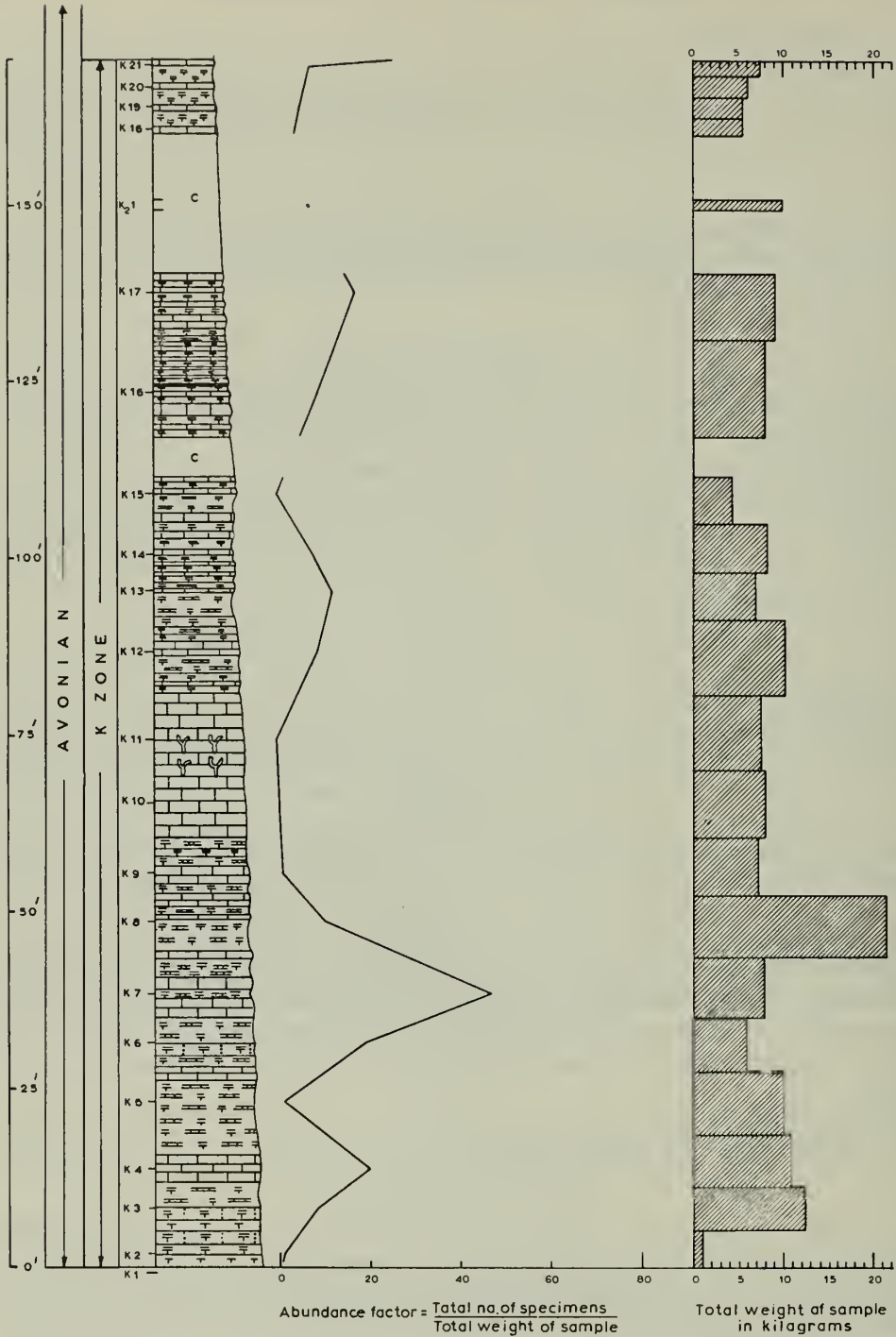


FIG. 59. Lithological section of the *Cleistopora* Zone in the Avon Gorge showing the abundance factor of conodonts in each sample, and the total weight of each sample dissolved in acetic acid. Samples K1-K17 were collected in the riverside section of the Avon Gorge (ST 556746). Samples K18-K21 were collected in the quarry 1 of the Avon Gorge (ST 557745), see Text-fig. 2.

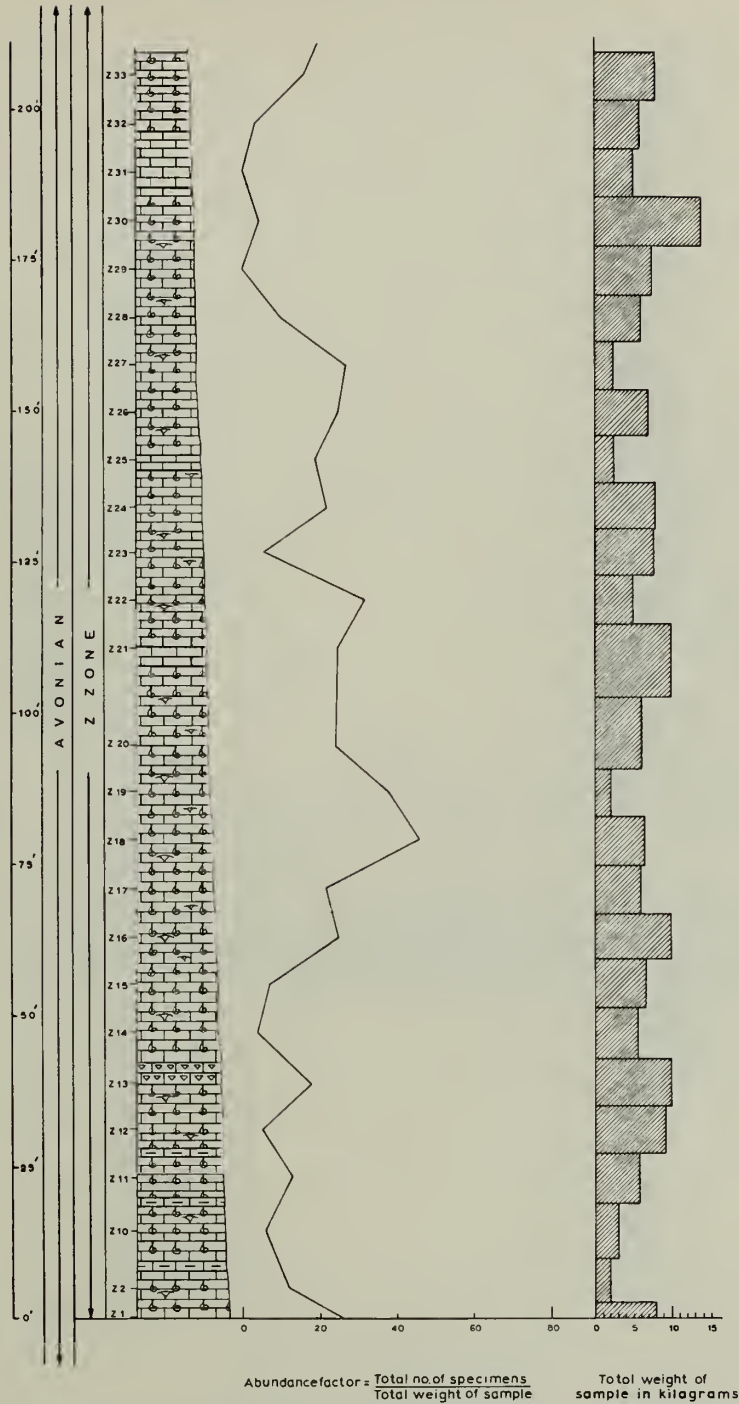


FIG. 60. Lithological section of the Lower and Upper *Zaphrentis* Zone in the Avon Gorge showing the abundance factor of conodonts in each sample, and the total weight of each sample dissolved in acetic acid. Samples Z 1–Z 10 were collected in Quarry 1 (ST 557745), Samples Z 11–Z 20 were collected in the Black Rock Quarry (ST 561747) and Samples Z 21–Z 33 were collected in Quarry 2 (ST 561747).

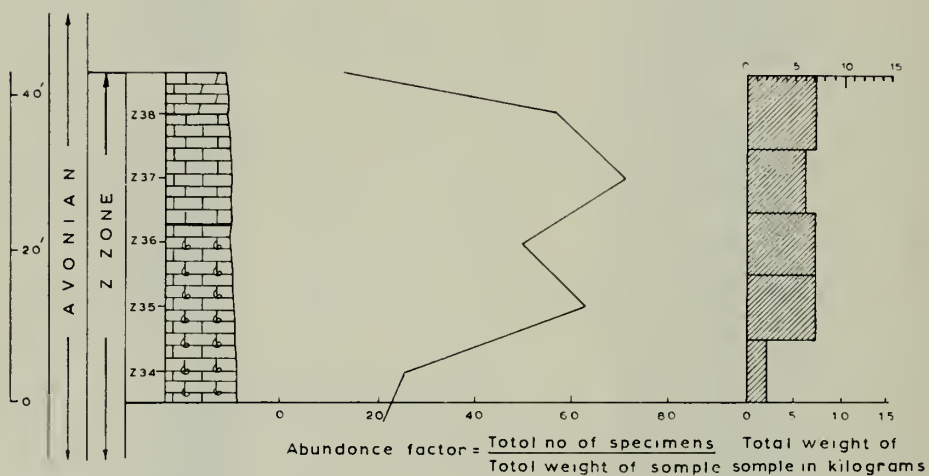


FIG. 61. Continuation of the lithological section of the Upper *Zaphrentis* Zone (γ Beds) in the Avon Gorge showing the abundance factor of conodonts in each sample dissolved in acetic acid. Samples Z 34-Z 38 were collected in Quarry 2 (ST 558745).

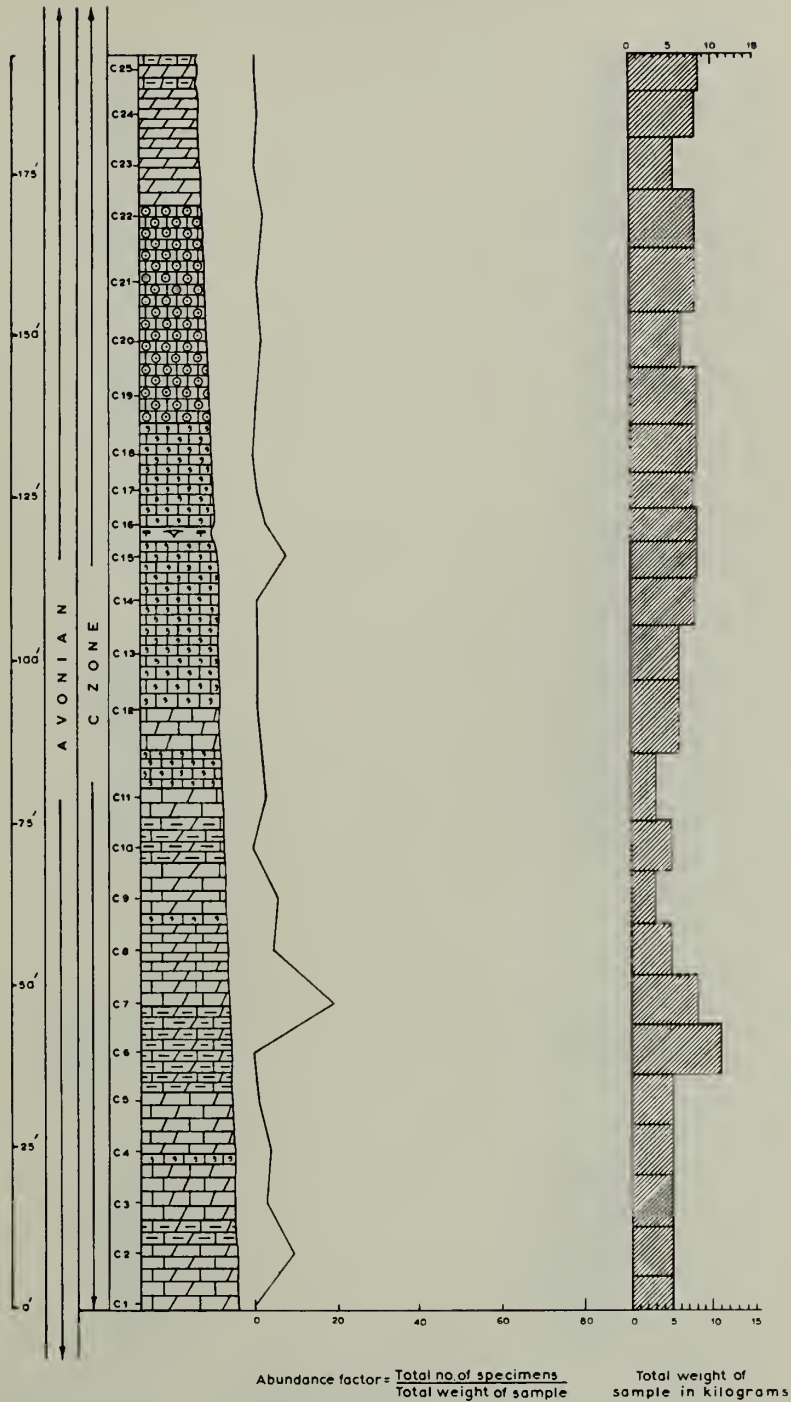


FIG. 62. Lithological section of the Lower *Caninia* Zone in the Avon Gorge showing the abundance factor of conodonts in each sample dissolved in acetic acid. Samples C 1-C 11 were collected in the Railway Cutting (ST 559745) and Samples C 12-C 25 in Quarry 3 (ST 560744).

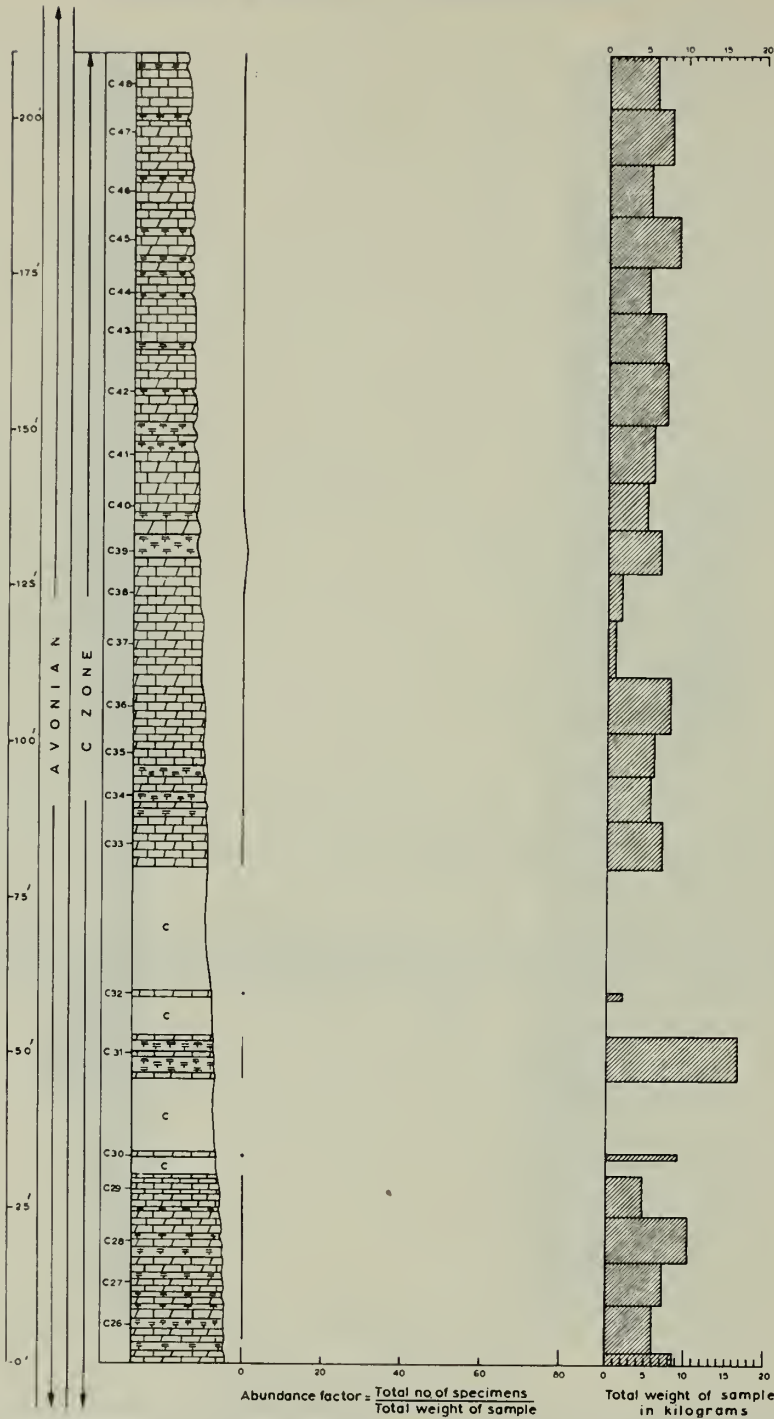


FIG. 63. Lithological section of the Upper *Caninia* Zone in the Avon Gorge showing the abundance factor of conodonts in each sample dissolved in acetic acid. Samples were collected from the roadside exposure (ST 562746).

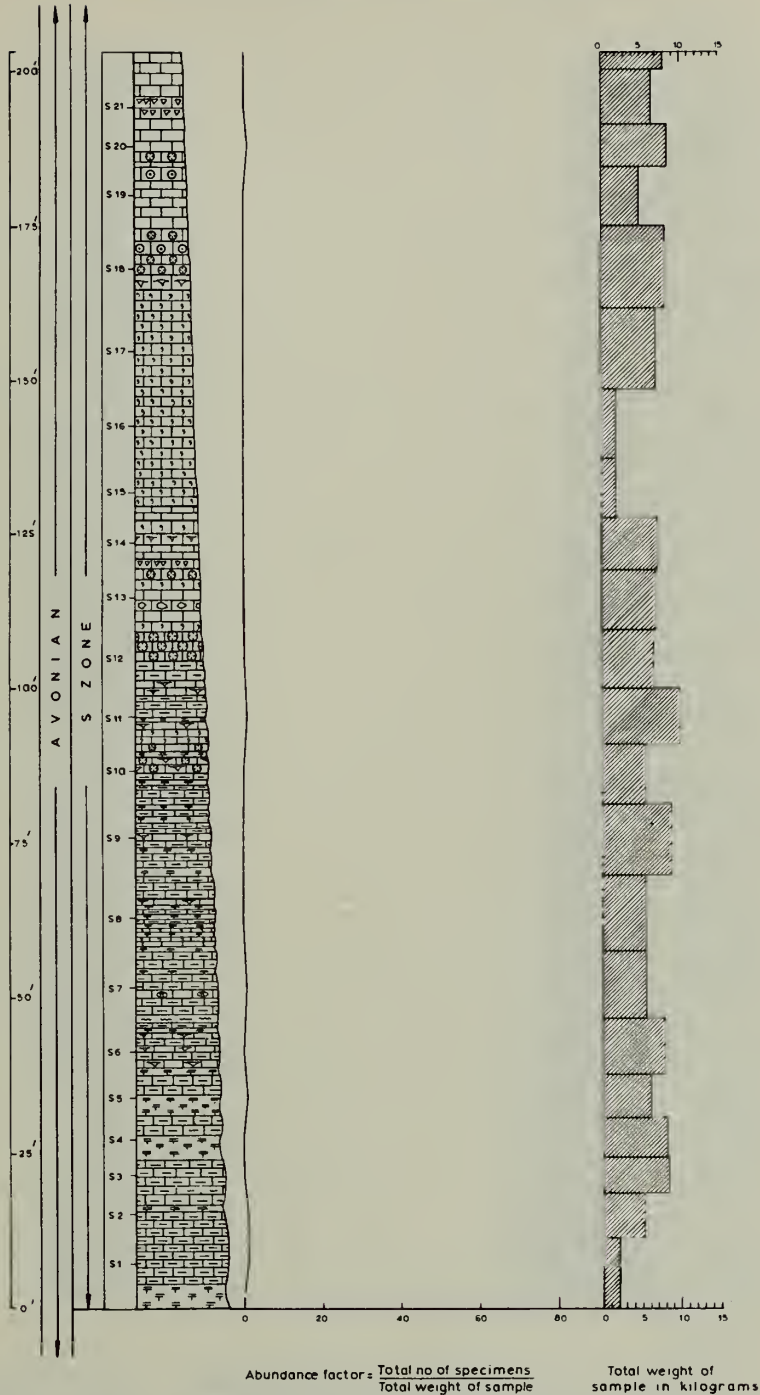


FIG. 64. Lithological section of the Lower and Upper *Seminula* Zone in the Avon Gorge showing the abundance factor of conodonts in each sample, and the total weight of each sample dissolved in acetic acid. The samples were collected in the Great Quarry (ST 563740).

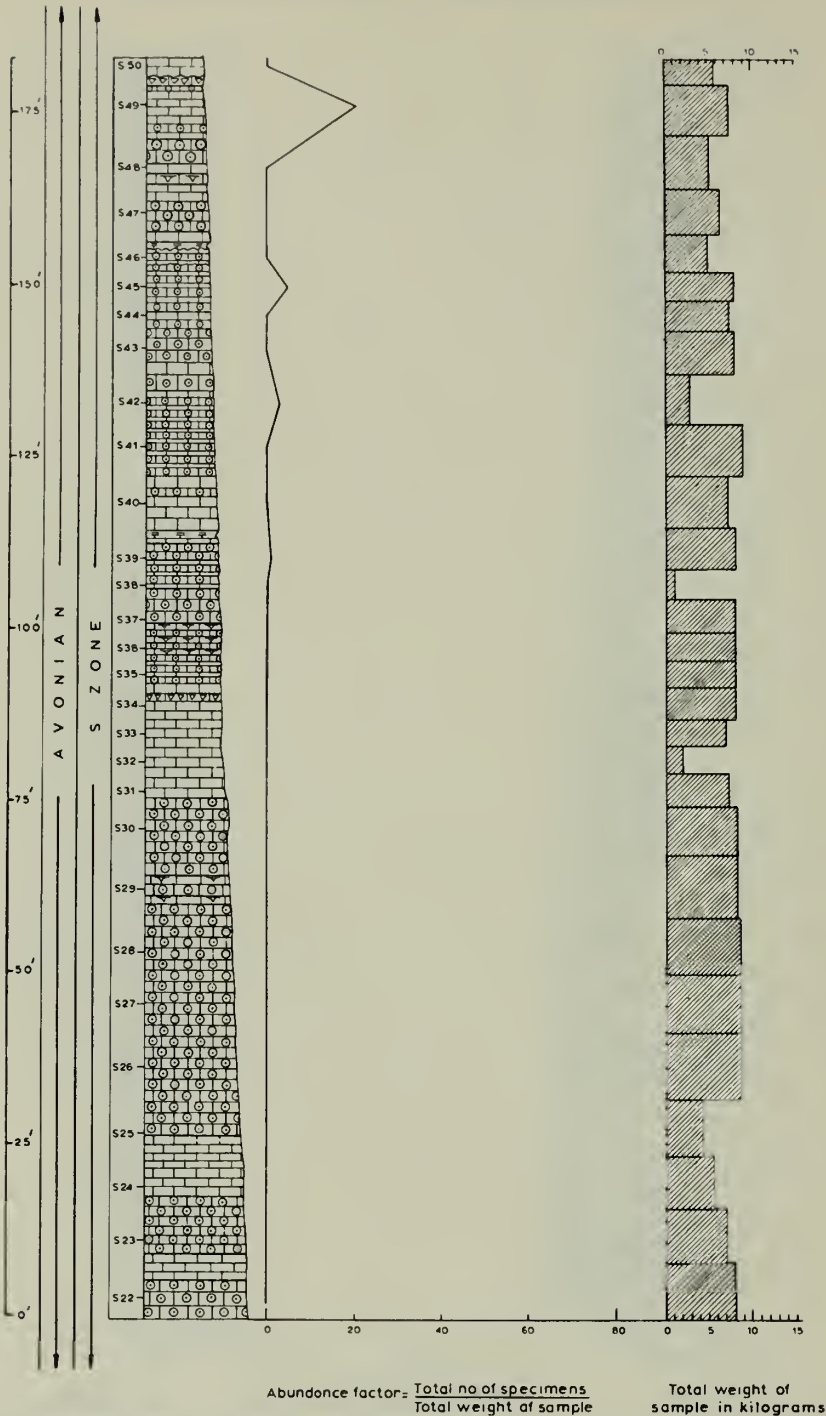


FIG. 65. Continuation of the lithological section of the upper part of the *Seminula* Zone in the Avon Gorge showing the abundance factor of conodonts in each sample dissolved in acetic acid. Samples S 22-S 30 were collected from the Great Quarry (ST 563740) and Samples S 31-S 50 from the riverside exposure (ST 562737).

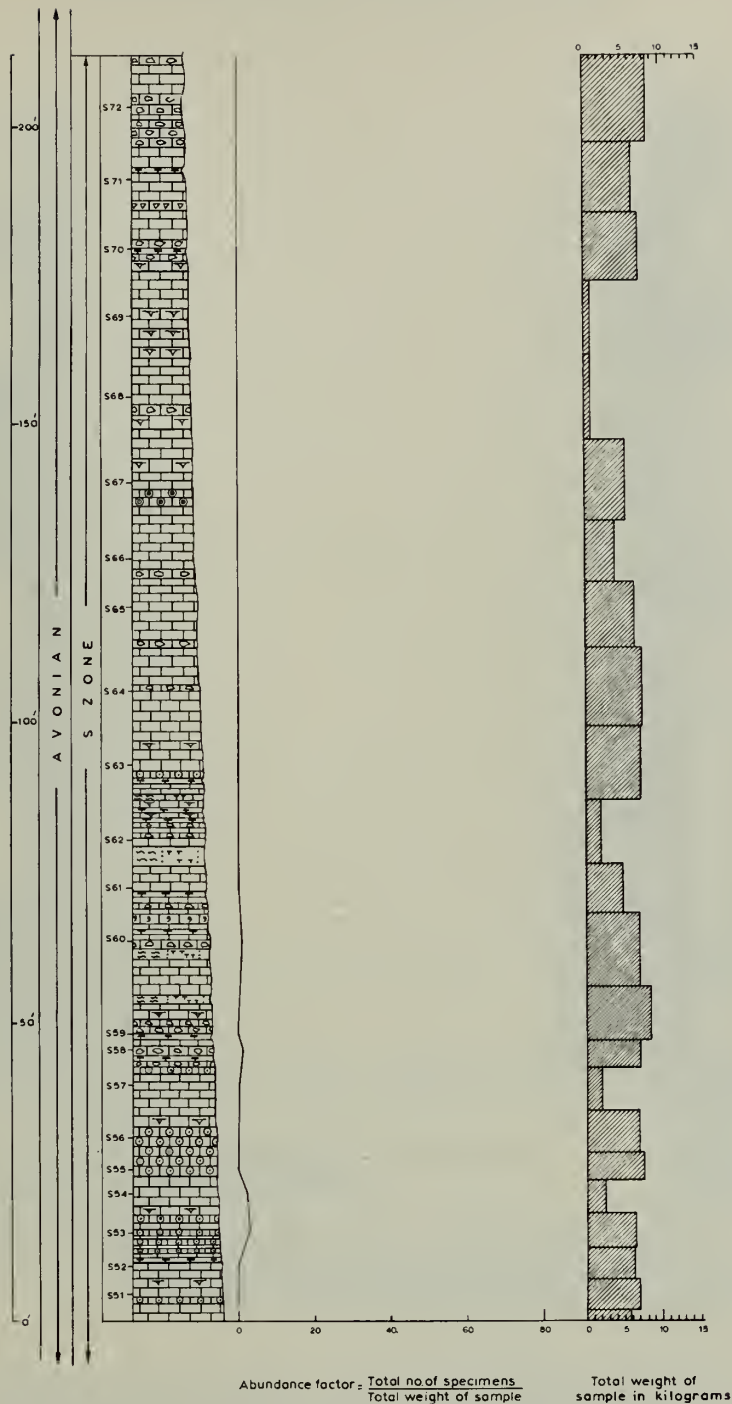


FIG. 66. Continuation of the lithological section of the uppermost part of the *Seminula* Zone and Concretionary Bed in the Avon Gorge showing the abundance factor of conodonts in each sample dissolved in acetic acid. Samples S 51-S 72 were collected from the riverside exposure (ST 562737).

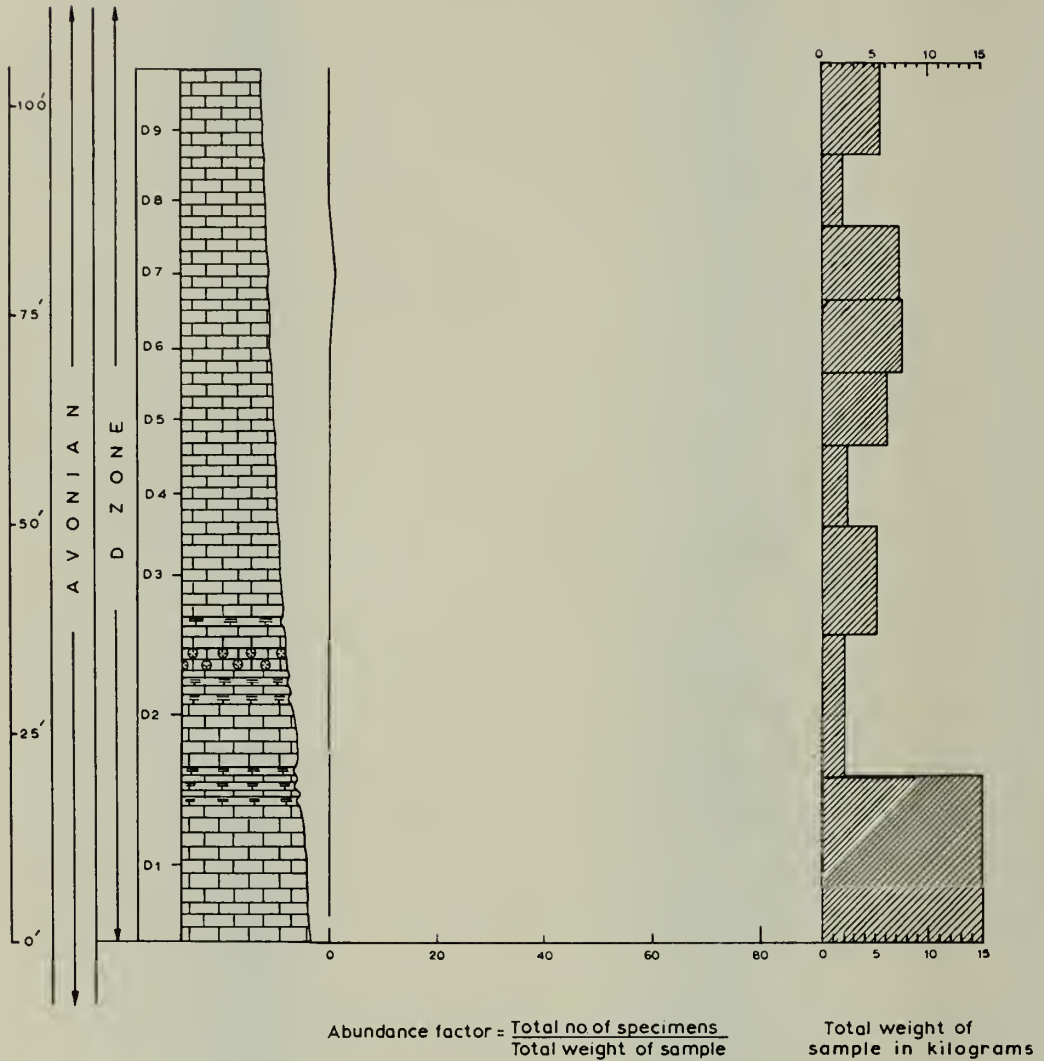


FIG. 67. Lithological section of the Lower *Dibunophyllum* Zone in the Avon Gorge showing the abundance factor of conodonts in each sample dissolved in acetic acid. Samples D 1-D 9 were collected from the roadside exposure (ST 564737).

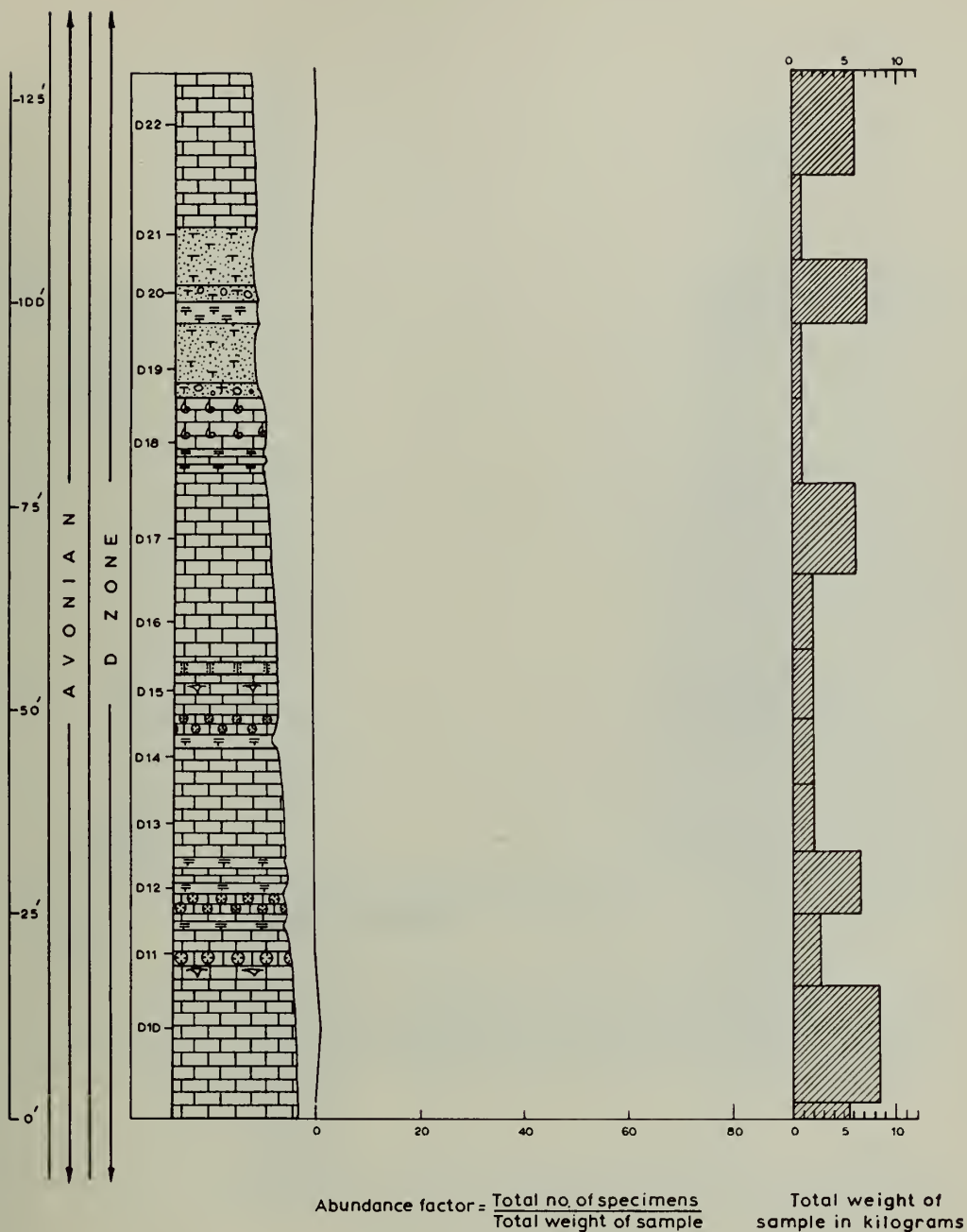


FIG. 68. Continuation of the lithological section of the *Dibunophyllum* Zone in the Avon Gorge showing the abundance factor of conodonts in each sample dissolved in acetic acid. Samples D to D 22 were collected from the roadside exposure (ST 564737).

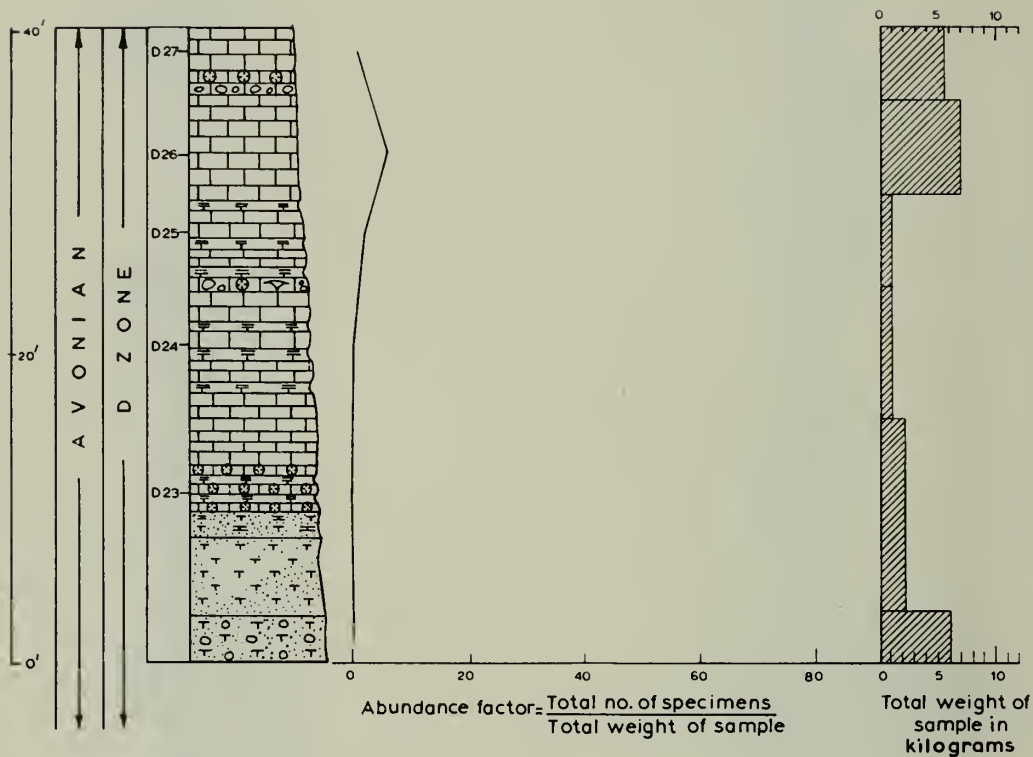


FIG. 69. Lithological section of the upper beds of the *Dibunophyllum* Zone in the Avon Gorge showing the abundance factor of conodonts in each sample dissolved in acetic acid. Samples D 23-D 27 were collected from south of Bridge Valley Road (ST 564736).

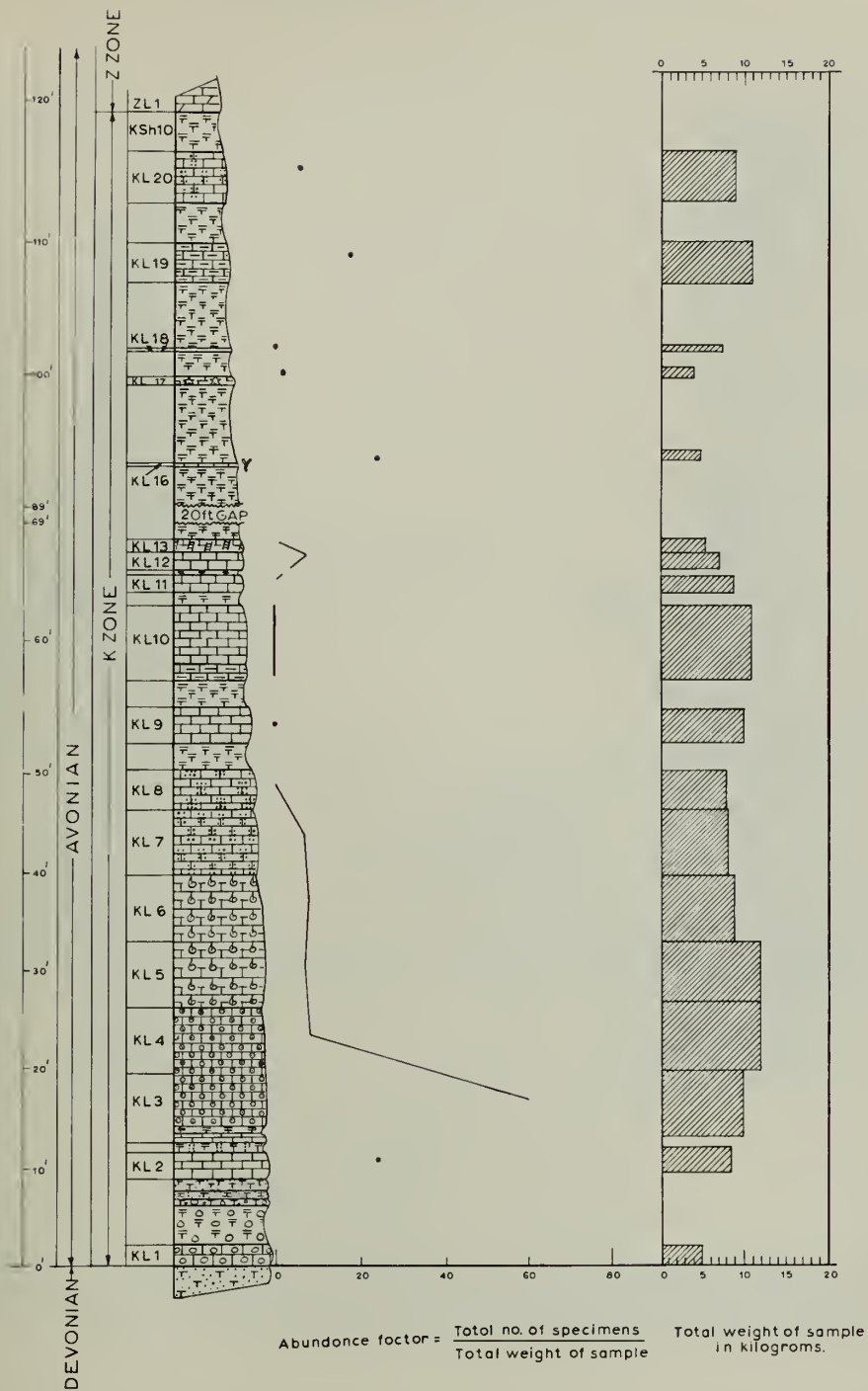


FIG. 70. Lithological section of the K Zone of the North Crop of the South Wales Coalfield showing the abundance factor of conodonts in each sample, and the total weight of limestone dissolved. For details of collecting localities see Fig. 7 and also p. 25.



FIG. 71. Lithological section of the Z and S₂ Zones of the North Crop of the South Wales Coalfield showing the abundance factor of conodonts in each sample, and the total weight of limestone dissolved. For details of collecting localities see Fig. 7 and also p. 25.

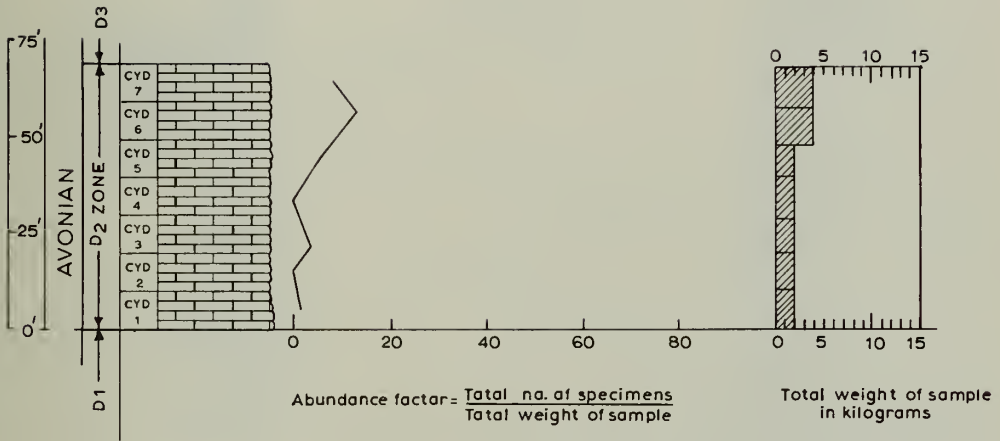


FIG. 72. Lithological section of the D₂ Subzone of the North Crop of the South Wales Coalfield showing the abundance factor of conodonts in each sample, and the total weight of limestone dissolved. For details of collecting localities see Fig. 7 and also p. 33.

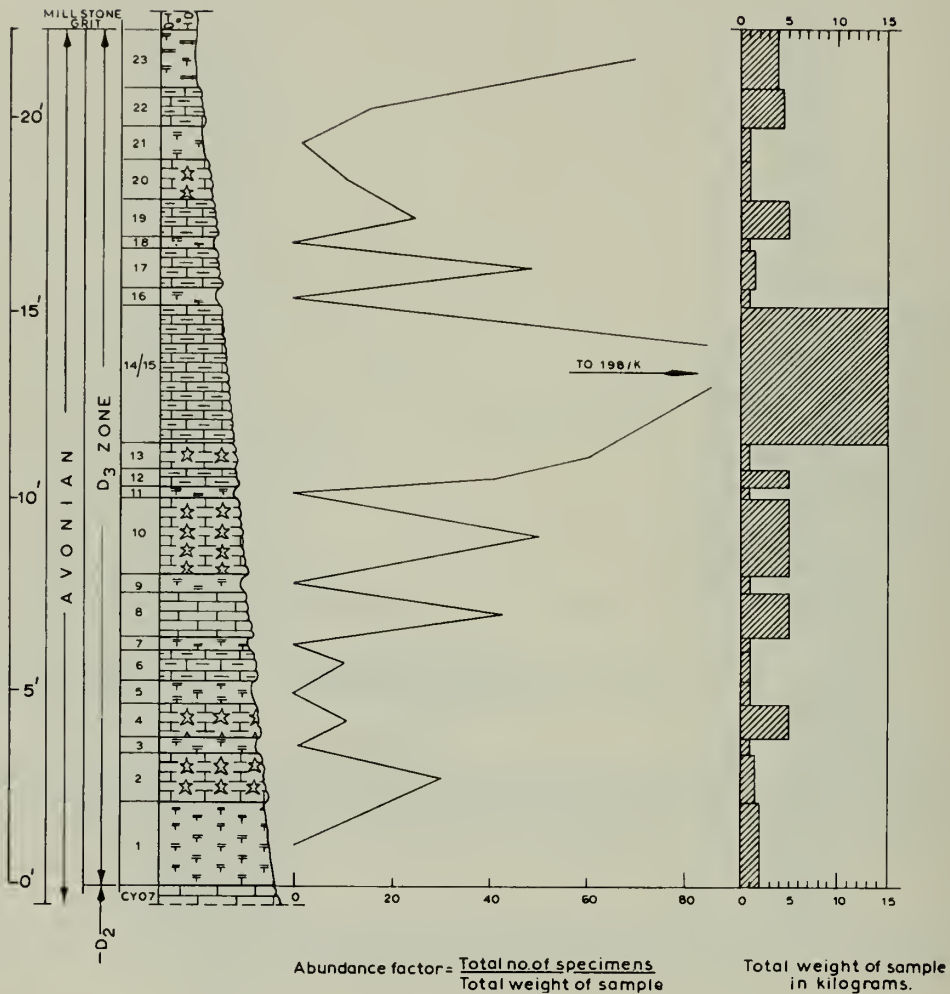


FIG. 73. Lithological section of the D₃ Subzone of the North Crop of the South Wales Coalfield showing the abundance factor of conodonts in each sample, and the total weight of limestone dissolved. For details of collecting localities see Fig. 7 and also p. 23.

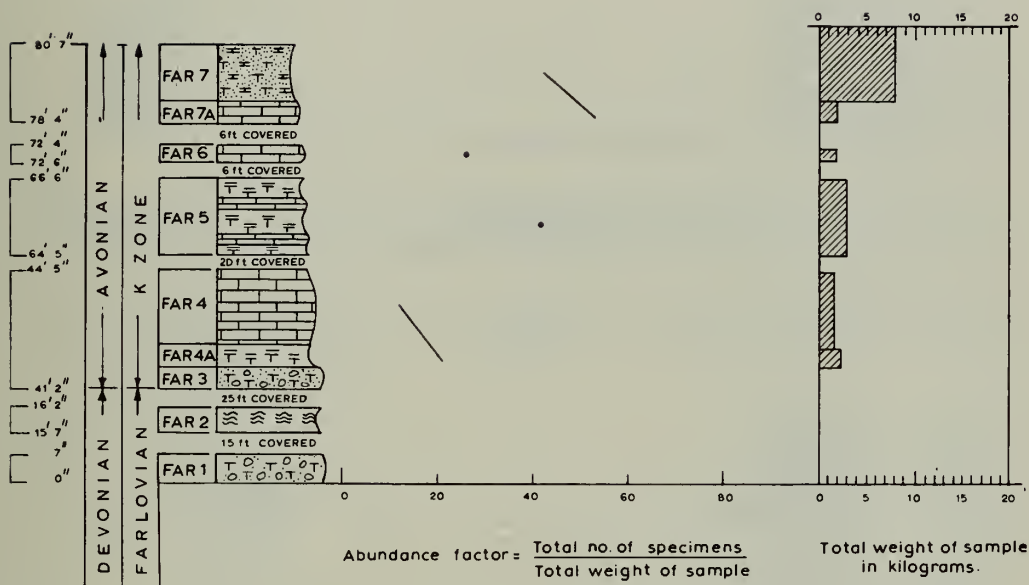


FIG. 74. Lithological section of the *Cleistopora* Zone at Farlow, Shropshire (Map reference SO 642808), showing the abundance factor of conodonts in each sample and the weight of each sample dissolved.

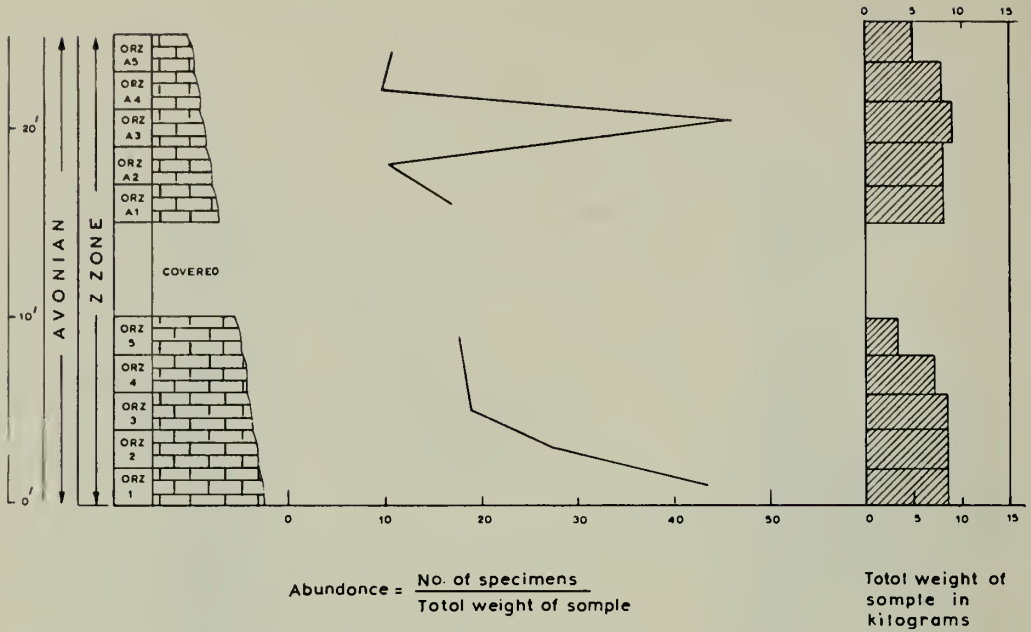


FIG. 75. Lithological section of the *Zaphrentis* Zone in Oreton Quarry, Shropshire, (SO 648806).

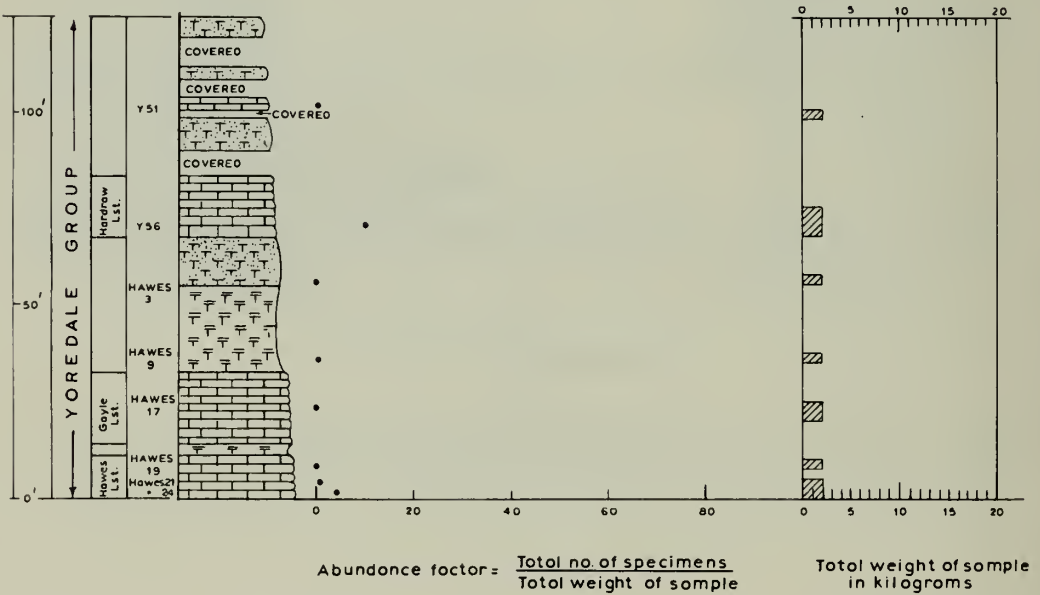


FIG. 76. Composite lithological section through the Yoredale Group (Hawes Limestone to base of Simonstone Limestone) in the Gayle Beck—Hawes area (34/864883).

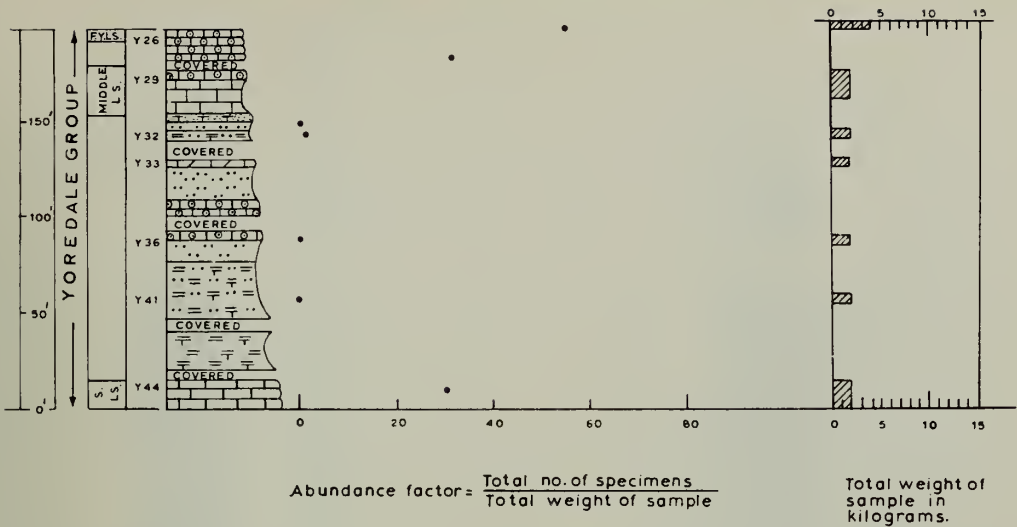


FIG. 77. Composite lithological section through the Yoredale Group (base of Simonstone Limestone to the top of the Five Yard Limestone inclusive) in the Snaizeholme—Hawes area (34/815840). S. Ls.=Simonstone Limestone : F.Y. Ls.=Five Yard Limestone.

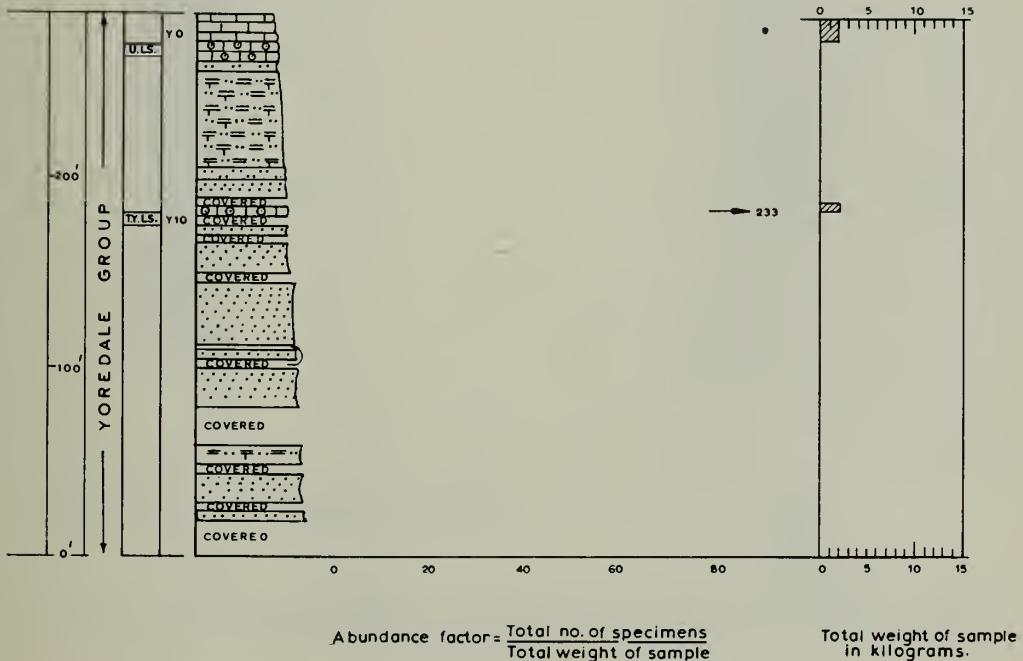


FIG. 78. Composite lithological section through the Yoredale Group (top of the Five Yard Limestone to the top of the Underset Limestone inclusive) in the Snaizeholme—Hawes area (34/815840). T. Y. Ls.=Three Yard Limestone : U. Ls.=Underset Limestone.

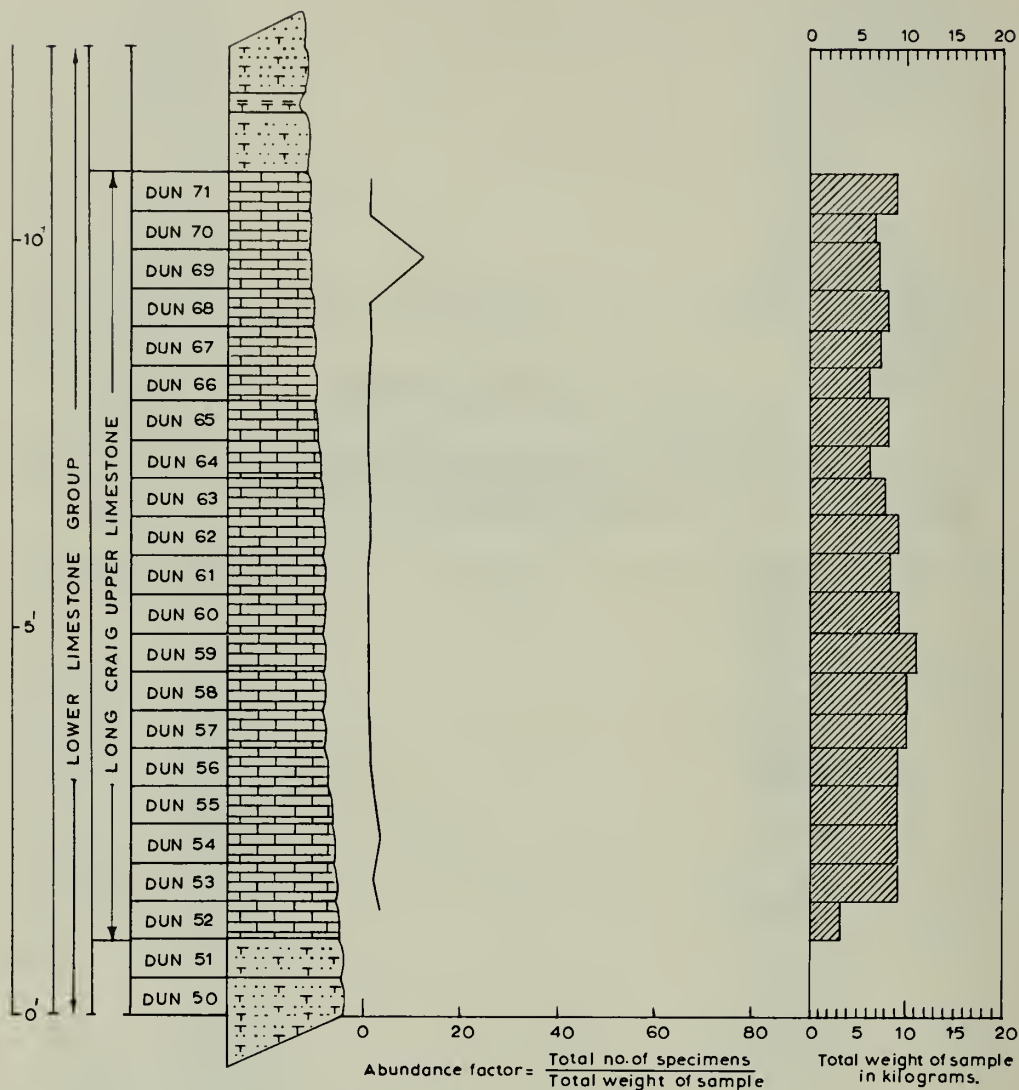


FIG. 79. Lithological section of part of the Lower Limestone Group in the Dunbar area : the Long Craig Upper Limestone, showing the abundance factor for each sample and the weight of each sample dissolved. For localities see p. 30.

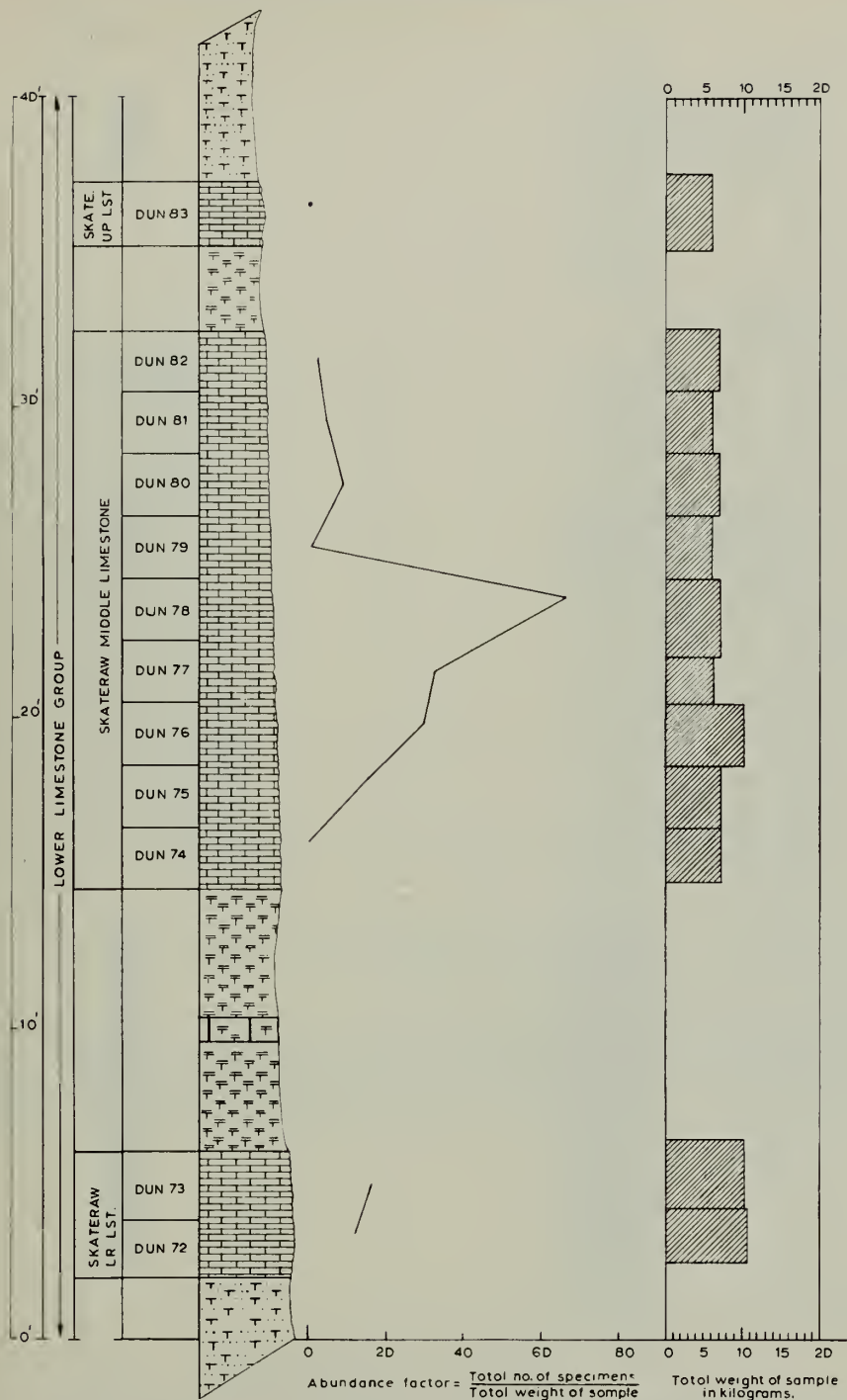


FIG. 80. Lithological section of part of the Lower Limestone Group in the Dunbar area : the Skateraw Lower Limestone to the Skateraw Upper Limestone, showing the abundance factor of each sample and the total weight of each sample dissolved. For localities see p. 30.

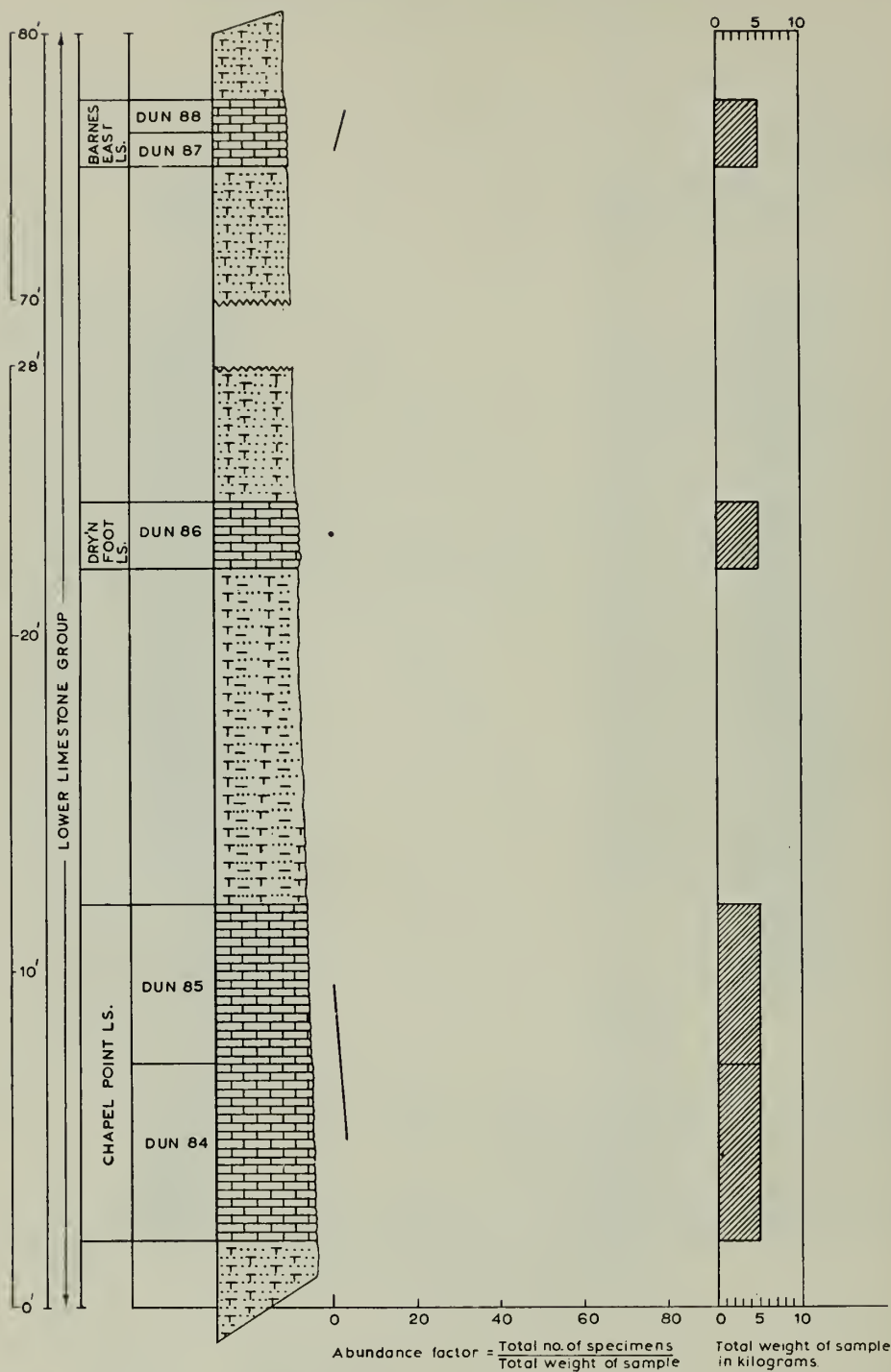


FIG. 81. Lithological section of part of the Lower Limestone Group in the Dunbar area : the Chapel Point Limestone to the Barnes East Limestone, showing the abundance factor of each sample and the weight of each sample dissolved. For localities see p. 30.

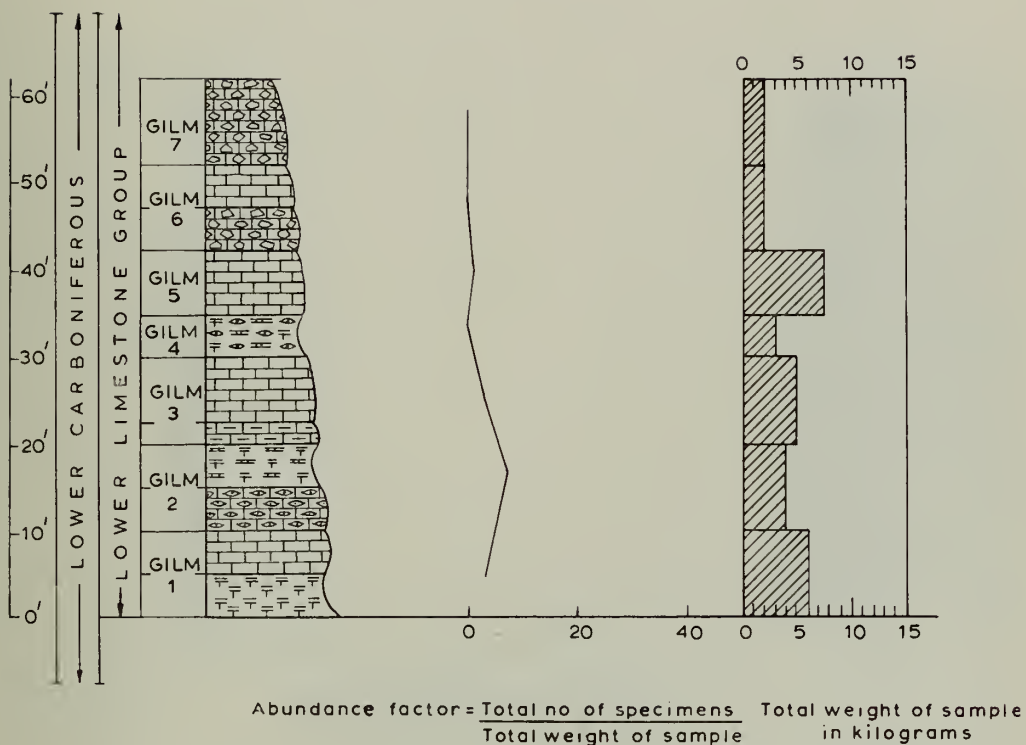


FIG. 82. Lithological succession of part of the Lower Limestone Group in Midlothian : the "Gilmerton" Limestone, showing the abundance factor of each sample and the weight of each sample dissolved. This limestone may not be the true Gilmerton Limestone (see p. 50). For localities see p. 30.

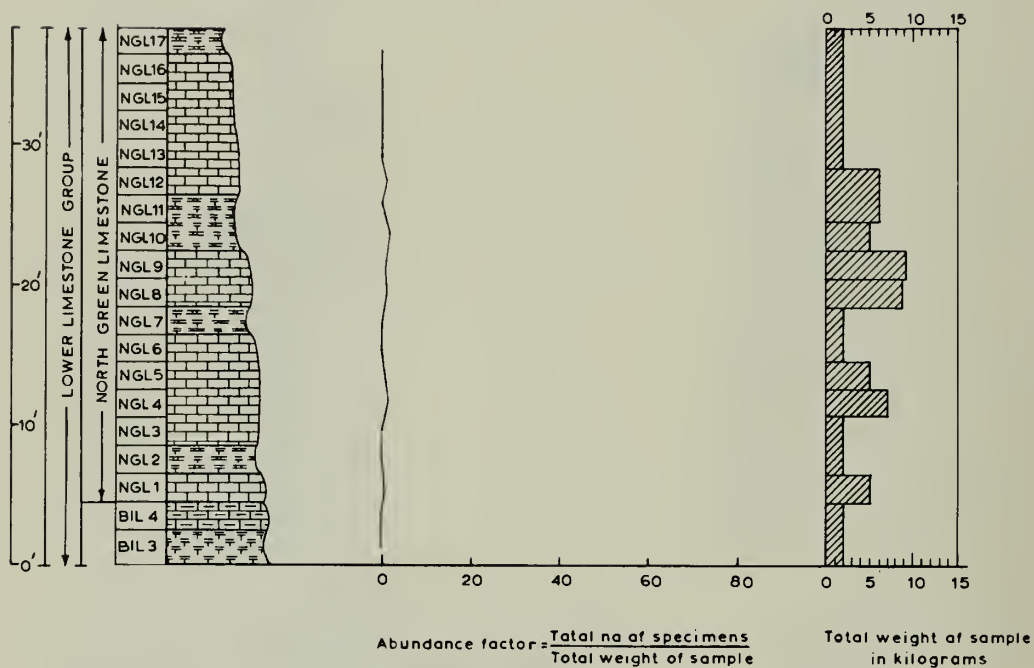


FIG. 83. Lithological section of part of the Lower Limestone Group in Midlothian : the North Greens Limestone, showing the abundance factor for each sample and the weight of each sample dissolved. For localities see p. 30.

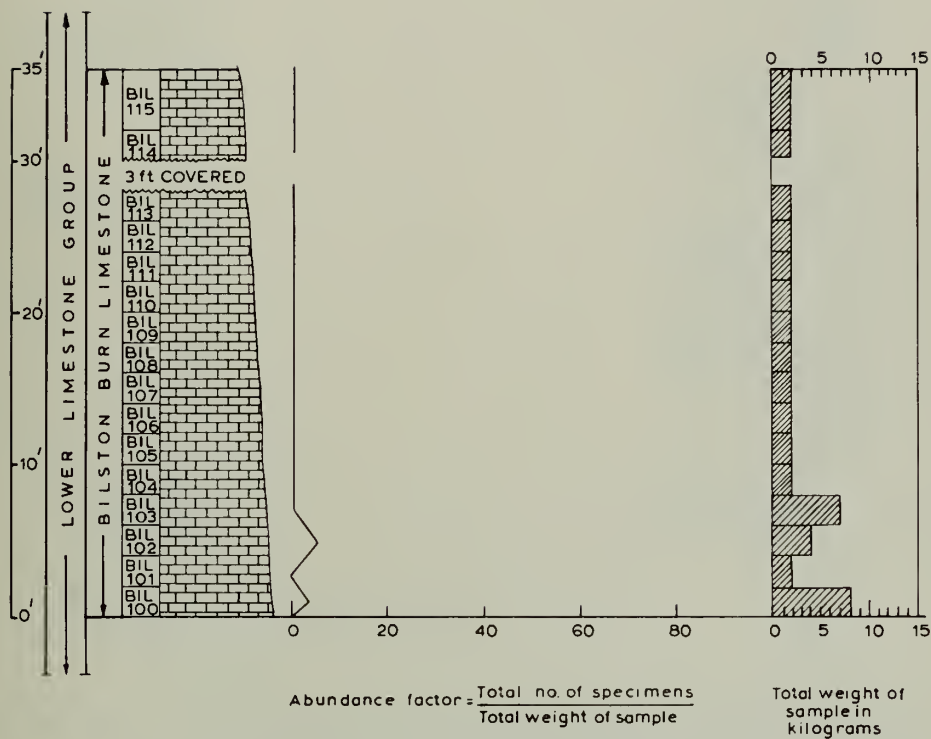


FIG. 84. Lithological section of part of the Lower Limestone Group in Midlothian: the Bilston Burn Limestone, showing the abundance factor and total weight of sample dissolved for each sample. For localities see p. 30.

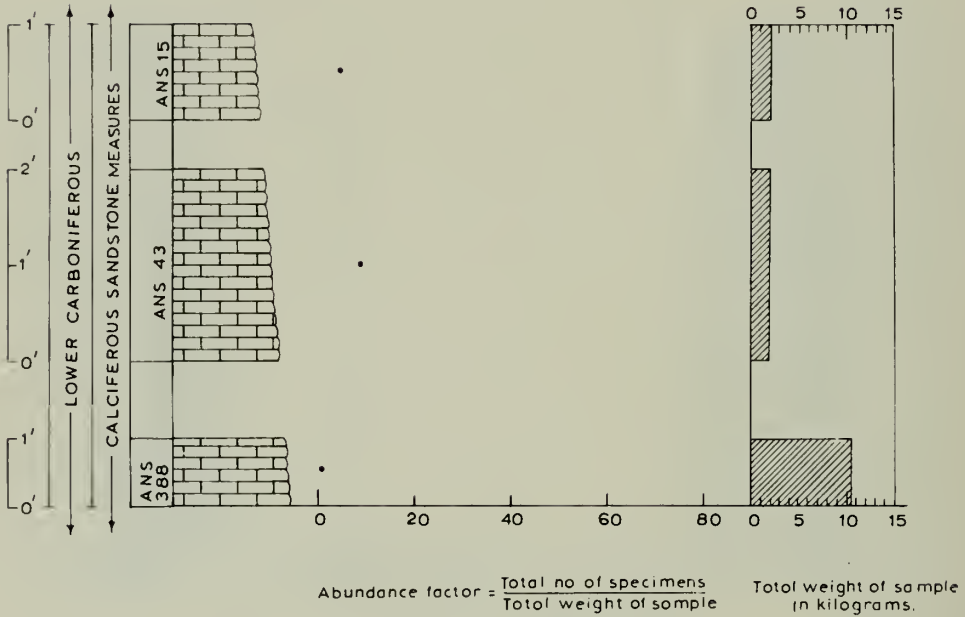


FIG. 85. Lithological succession of part of the Calciferous Sandstone Series of East Fife, showing the fossiliferous limestones in the lower part of the succession. Coast section from Hurllet Limestone near Coalfarm to Anstruther (NO 548027). Sample numbers refer to detailed section given by J. W. Kirkby in Geikie (1902), p. 77 ff.

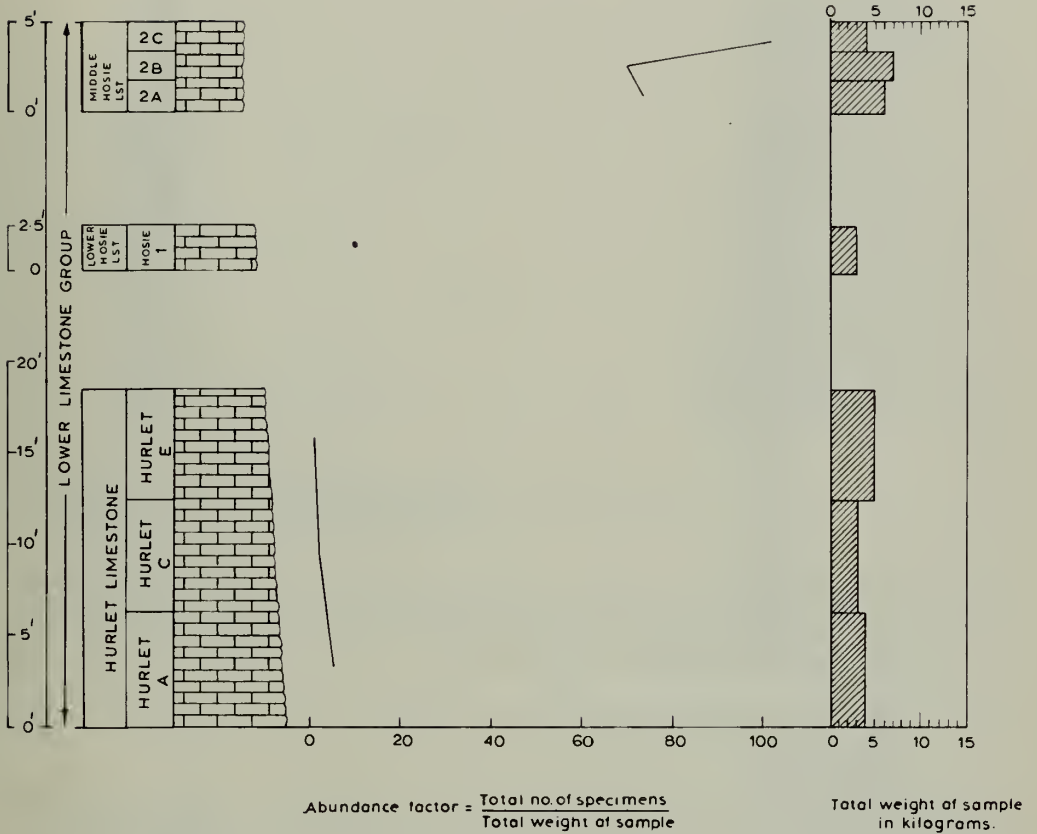


Fig. 86. Continuation of coast exposure of Fig. 85. Lithological section of part of the Lower Limestone Group in East Fife : Hurlet and Hosie Limestones, showing abundance factor for each sample and weight of each sample dissolved.

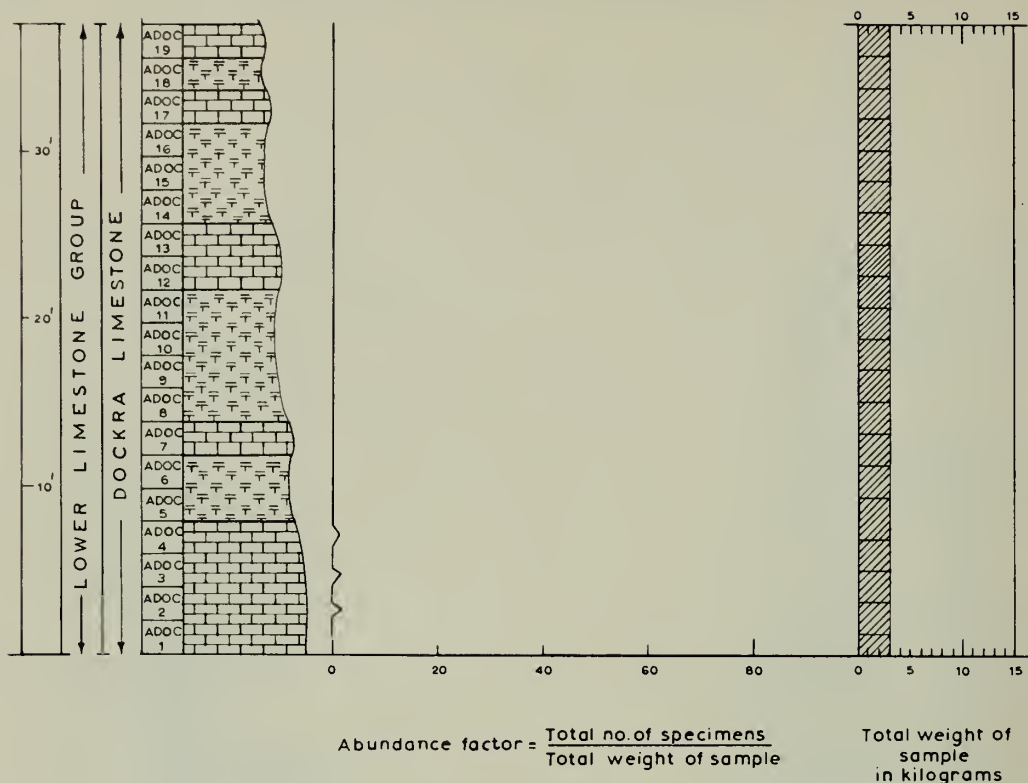


FIG. 87. Lithological section of part of the Lower Limestone Group in North Ayrshire : the Dockra Limestone, showing abundance factor for each sample and weight of each sample dissolved. For localities see p. 30.

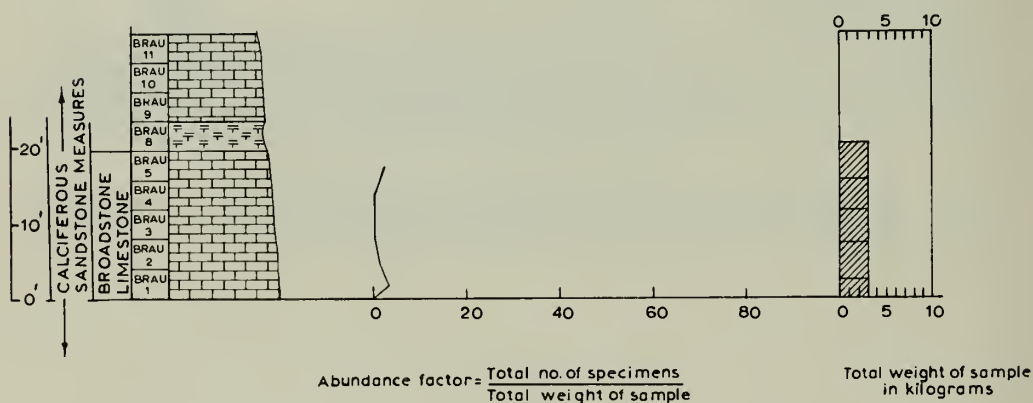


FIG. 88. Lithological section of part of the Calciferous Sandstone Series in North Ayrshire, showing the abundance factor of each sample and the total weight of each sample dissolved. For localities see p. 30.

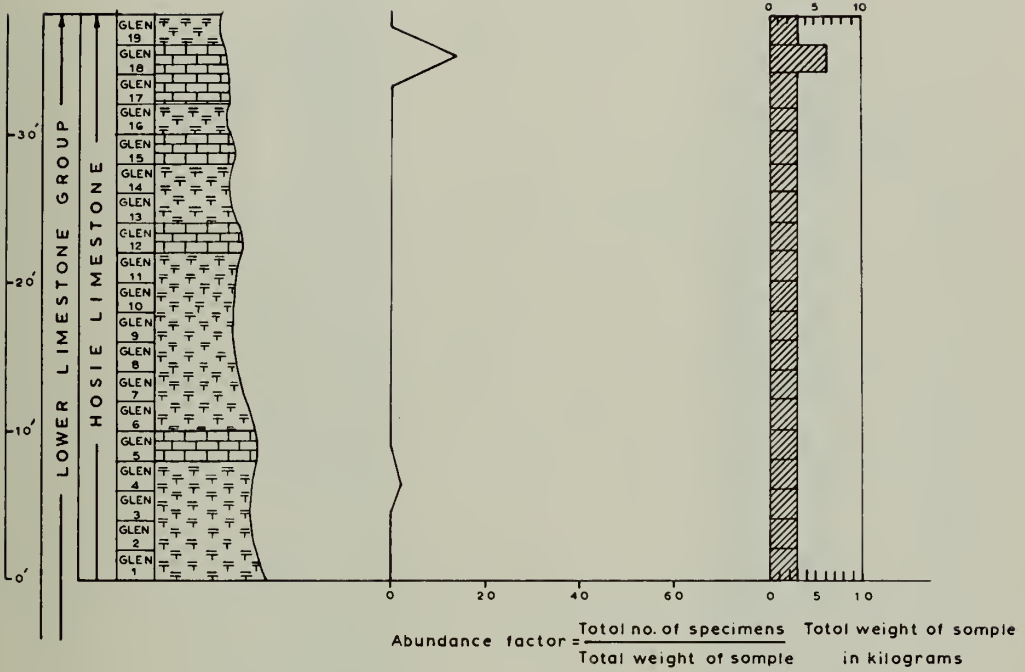


FIG. 89. Lithological section of part of the Lower Limestone Group of North Ayrshire : the Hosie Limestone, showing the abundance factor for each sample and the weight of each sample dissolved. For localities see p. 30.

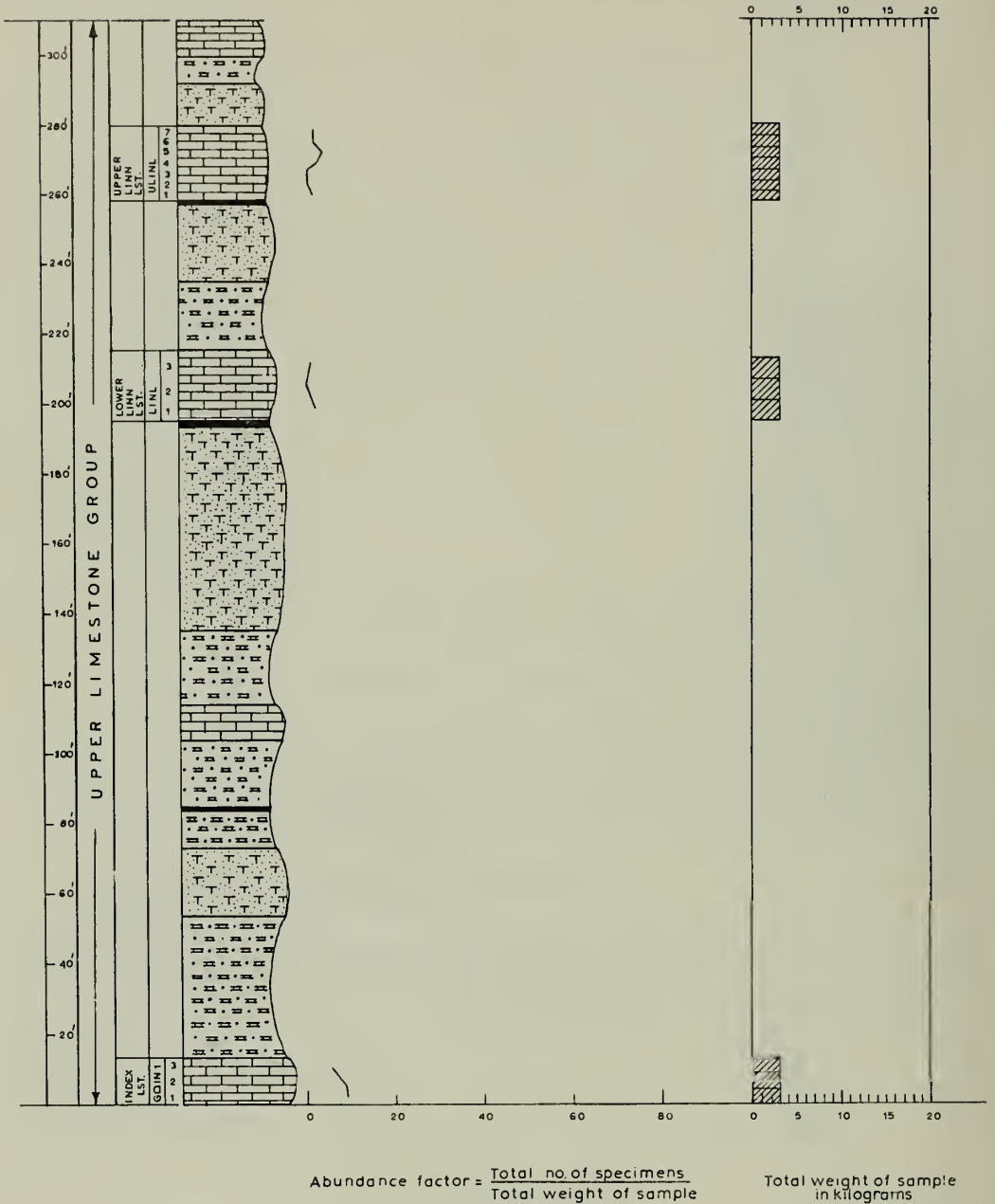


FIG. 90. Lithological section of part of the Upper Limestone Group of North Ayrshire : the Index Limestone to the Upper Linn Limestone, showing the abundance factor for each sample and the weight of each sample dissolved. For localities see p. 30.

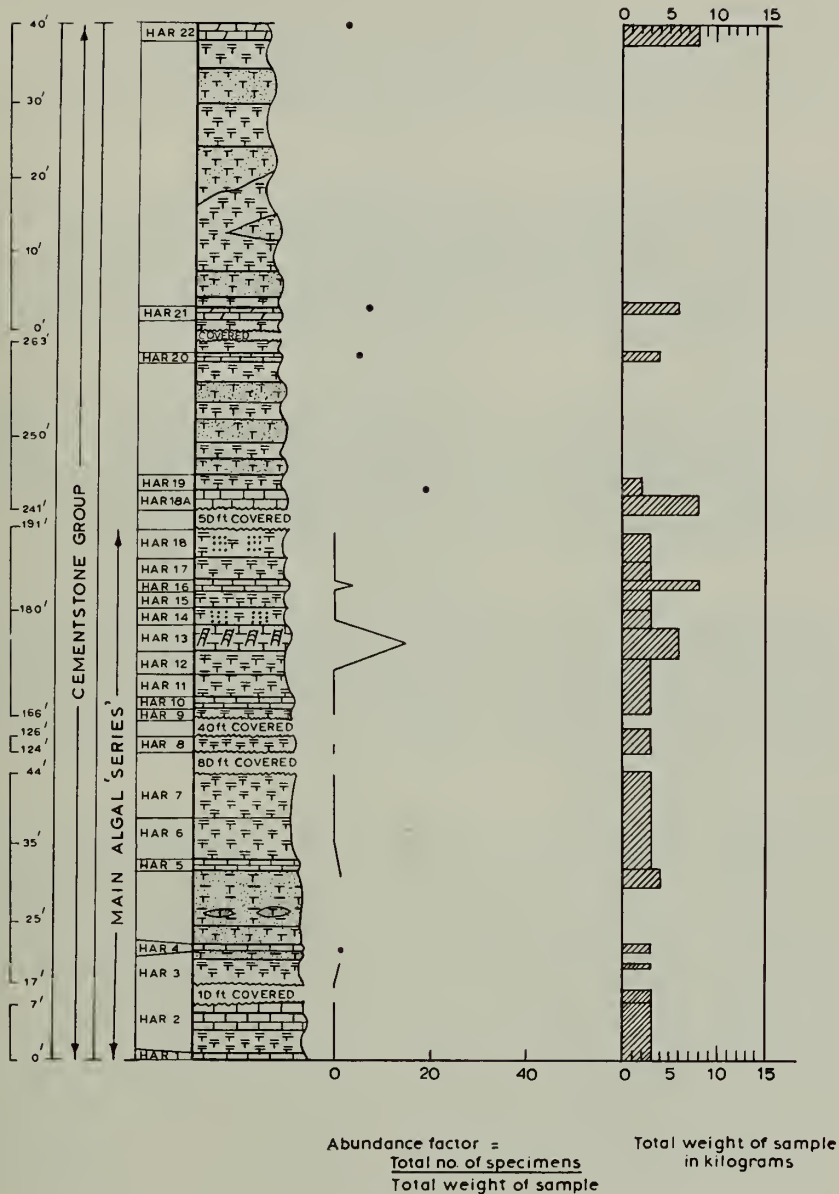


FIG. 91. Lithological section of the Lower Algal Limestone "Series" of Harden Burn, Roxburghshire, (NY 517907) showing the abundance factor for each sample and the weight of each sample dissolved.

Mid-Avonian unconformity in some places in the North Crop, and the absence of conodonts in others, does not allow comparisons of the middle part of the succession, although the uppermost Z of the Avon Gorge is younger than that of the North Crop. The base of the D₂ Subzone corresponds in both the Avon Gorge and the North Crop. Few D₂ or D₃ conodonts have been recovered from the Avon Gorge (Figs. 67-69).

Shropshire

The lowest K strata at Farlow appear to be younger than those of the Avon Gorge, or the North Crop. The Shropshire K Zone strata represent a very condensed deposit. The higher part of the K Zone at Farlow is equivalent to the Lower Z of the Avon Gorge. The Z Zone at Farlow represents the *Spathognathodus costatus costatus*-*Gnathodus delicatus* Zone.

Yorkshire

The lowermost Yoredale limestones (the Gayle and the Hawes) have yielded few conodonts. The overlying Hardraw Scar Limestone and Simonstone Limestone fall within the *Gnathodus mononodosus* Assemblage Zone, and the Middle and Five Yard Limestones within the *Gnathodus girtyi collinsoni* Assemblage Zone.

Scotland

A correlation is suggested between the Fife, Midlothian, Ayrshire, Dunbar and Glengarnock successions, and between these and the South Western Province. The Scottish sections all fall within the *Gnathodus mononodosus* or *Gnathodus girtyi collinsoni* Zones, except for the lowest part of the Ayrshire succession and the Lower Algal "Series" of Roxburghshire. Details of the correlations are given in Fig. 15.

(h) *Intercontinental correlation*

A critical review of North American and European Lower Carboniferous conodont faunas is given (p. 52), and the correlation of these with the British Avonian is summarized in Figs. 12, 16. The K Zone of the Avonian, represented by the two lowest conodont zones and by the lower part of the *Spathognathodus* cf. *S. robustus*-*S. tridentatus* Zone, is probably equivalent to the Lower Hannibal-Upper Chouteau succession of the Mississippi Valley (Cu I-Cu II α). This would imply a very considerable unconformity below the "Sedalia Formation" (Lower Cu II β - γ) which is correlated with the *Polygnathus lacinatus* Zone of the Upper Z₂ Beds. An alternative correlation, based upon the first appearance of *Gnathodus delicatus*, would equate the *Spathognathodus costatus costatus*-*Gnathodus delicatus* Zone of the Middle Z Zone with the Upper Chouteau (Cu II α) (p. 56). The highest Z Zone is equivalent to the Fern Glen and lower part of the Burlington Formations (Middle Cu II β - γ).

The C₁ Subzone of the Avonian is of Upper Cu II β - γ -Lower Cu II δ (Middle and Upper Burlington) age, and the C₂S₁ and S₂ Subzones of Upper Cu II δ age. (Keokuk to Lower St. Louis).

The D₁ Subzone is of Cu III α age, the D₂ Subzone of Cu III α -Cu III β age, and the D₃ Subzone of Cu III β - γ age.

LEGEND FOR LITHOLOGICAL SECTIONS

CLASTIC SEDIMENTARY ROCKS



Gravel



Conglomeratic arkose



Coarse-grained sandstone



Conglomeratic sandstone



Calcareous sandstone



Slightly sandy formation



Siltstone



Clay



Stratified clay



Argilloceous formation



Shale



Thin coal bed



Fine clay



Shale lenses



Silt



Carbonaceous shale

OTHER SEDIMENTARY ROCKS AND STRUCTURES



Limestone



Fossil-fragment limestone



Detrital limestone



Limestone breccio



Oolitic limestone



Pisolitic limestone



Crystalline limestone



Sucrose limestone



Dolomite



Dolomitic limestone



Calcareous formation



Marl



Argillaceous limestone



Calcareous lenses



Dolomitic lenses

GENERAL



Lithified formation



Covered



Red beds



25% sand
75% clay



Lateral transition



Chert



Cherty formation



Concretions



Algae



Corals



Brachiopods



Fossils in general



Bryozoa



Crinoids

FIG. 92. Composite legend for the lithological sections shown in the text.

(i) *Systematic palaeontology*

The total fauna described includes some 25,000 identifiable specimens, referable to 167 species. These are described and illustrated, and their precise stratigraphical ranges recorded. Two new named genera, 40 new species and 13 new subspecies are recognized.

(j) Detailed lithological sections and abundance figures are included for each part of the succession. Range charts are also provided.

VIII. ACKNOWLEDGMENTS

We are deeply indebted to our colleagues in the Geology Department, University College of Swansea, for help and advice during the course of this study. Mr. T. R. Owen has given us the benefit of his extensive knowledge of the Avonian rocks of South Wales, and has been a particular help to us in planning our collecting in that area. Mr. Brian Simpson has assisted us with various aspects of the technical work involved in the study. We owe a particular debt of gratitude to Mrs. Shirley Osborn and Mr. Michael Reynolds, for their patient help in rock processing, to Miss Sonia Kostromin for her enormous secretarial help, to Mr. Stanley Osborn for his skilful photography, to Mrs. Greir Lewis and Mrs Beryl Fisher who have prepared the text-figures, to Miss Rhiannon Watkins for typing, and to Miss Veronica Arlen and Mr. H. A. H. McKee for their editorial help.

We have been greatly helped by the generous advice of a large number of friends in various countries, who have willingly discussed problems of systematics and correlation with us, and have in some cases provided toptype material for comparison. We particularly wish to thank Dr. Gunther Bischoff of Gewerkshaft Elwerath Erdolwerke, Hannover, Dr. Charles W. Collinson of the Illinois Geological Survey, Dr. Raphael Conil of the Catholic University of Louvain, Professor Brian F. Glenister of the University of Iowa, Professor F. Hodson of Southampton University, Dr. John Huddle of the U.S.G.S., Washington, Dr. Huw Jenkins of Sydney University, Dr. Gilbert Klapper of Pan American Petroleum Corporation, Tulsa, Oklahoma, Dr. M. Lys of the Institut Francais du Pétrole, Dr. S. C. Matthews of the University of Bristol, Dr. Klaus-Dieter Meischner, of the University of Gottingen, Dr. D. Moore of Southampton University, Dr. Carl Rexroad of the Indiana Geological Survey, Dr. James W. Scatterday of the State University of New York at Geneseo, Dr. Trevor Walker of Long Beach College, California, Mr. R. B. Wilson of the I.G.S., Edinburgh, and Dr. Willi Ziegler of the Geologisches Landesamt Nordrhein-Westfalen.

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X. APPENDIX

(a) SAMPLE REGISTER

The following prefixes are used for sample numbers :

KL	K Zone	North Crop Limestone
K Sh	K Zone	North Crop Shale
ZL	Z Zone	North Crop Limestone (ten feet samples)
ZLA	Z Zone	North Crop Limestone (two feet samples)
Z Sh	Z Zone	North Crop Shale
CL	C ₂ S ₁ Zone	North Crop Limestone
C Sh	C ₂ S ₁ Zone	North Crop Shale
SL	S ₂ Zone	North Crop Limestone
1 DL	D ₁ Zone	North Crop Limestone
CYD	D ₂ Zone	North Crop (Craig-y-Dinas)
2 DL	D ₂ Zone	North Crop Limestone
2D Sh	D ₂ Zone	North Crop Shale
3D	D ₃ Zone	North Crop Owen & Jones numbers
FAR	K Zone	Farlow
ORZ	Z Zone	Farlow (Oreton)
HAR	C ₁ Zone ?	Harden Burn, Roxburgh (Lower Algal limestone)
DUN	L. Limestone Group	Dunbar
GILM	Gilmerton Limestone	Midlothian
BIL 1-4	Beds below North Greens Limestone	
BIL 100+	Bilston Burn Limestone	Midlothian
NGL	North Greens Limestone	Midlothian
VEX	Lower Vexhim Limestone	Midlothian
ANS	Calciferous Sandstone Series	Fife
HOSIE	Hosie Limestones	Fife
HURLET	Hurlet Limestone	Fife
GO-IN	Index Limestone	Ayrshire
DR-IN		
LIN-L	Lower Linn Spout Limestone	Ayrshire

U-LIN	Upper Linn Spout Limestone	Ayrshire
BRAU	Broadstone Limestone	Ayrshire
ADOC	Dockra Limestone	Ayrshire
GLEN	Hosie Limestones	Glengarnock, Ayrshire
MAC	Lower Limestone Series	Macrihanish, Argyll
SCC	C Zone	Fall Bay, Gower, South Wales
GUD	Upper Devonian Germany, Hönnetal	
	Upper <i>costatus</i> Zone to VI	
K	K Zone	Avon Gorge Limestone
Z	Z Zone	Avon Gorge Limestone
C	C Zone	Avon Gorge Limestone
S	S Zone	Avon Gorge Limestone
D	D Zone	Avon Gorge Limestone
Y	Yoredale Limestone	Yorkshire

Map references for all localities are given in the text-figure explanations and on p. 18-31.

REGISTER OF FIGURED SPECIMENS

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 36	<i>Angulodus walrathi</i> (Hibbard)	KL 19
X 37	sp. nov. B	ZLA 14
X 38	sp. nov. C	ZLA 10
X 39	sp. nov. C	ZLA 14
X 40	sp. nov. D	ZLA 11
X 41	sp. nov. D	ZLA 11
X 42	<i>Apatognathus varians</i> Branson & Mehl	ZLA 13
X 43	sp. nov. A	ZLA 13
X 44	<i>chauliodus</i> Varker	HOSIE 2 B
X 45	<i>bladus</i> sp. nov.	CYD 7A
X 46	<i>bladus</i> sp. nov.	CYD 7A
X 47	<i>scalenus</i> Varker	HOSIE 2 B
X 48	<i>scalenus</i> Varker	HOSIE 2 B
X 49	<i>scalenus</i> Varker	HOSIE 2 B
X 50	<i>petilus</i> Varker	HOSIE 2 A
X 51	<i>petilus</i> Varker	HOSIE 2 A
X 52	<i>petilus</i> Varker	HOSIE 2 A
X 52	<i>petilus</i> Varker	3D 14/15 XL 13
X 54	<i>geminus</i> (Hinde)	DUN 54
X 55	<i>geminus</i> (Hinde)	DUN 54
X 56	<i>geminus</i> (Hinde)	HOSIE 2 B
X 57	<i>geminus</i> (Hinde)	HOSIE 2 A
X 58	cf. <i>libratus</i> Varker	HOSIE 2 A
X 59	<i>Cavusgnathus charactus</i> (Rexroad)	HAR 13
X 60	<i>Apatognathus</i> sp.	HOSIE 2 A

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 61	<i>Cavusgnathus charactus</i> (Rexroad)	HAR 13
X 62	<i>charactus</i> (Rexroad)	HAR 13
X 63	<i>convexus</i> Rexroad	3D 14/15
X 64	<i>cristatus</i> Branson & Mehl	3D 22
X 65	<i>naviculus</i> (Hinde)	HOSIE 2 B
X 66	<i>naviculus</i> (Hinde)	Gilm 2
X 67	<i>naviculus</i> (Hinde)	3D 14/15
X 68	<i>naviculus</i> (Hinde)	3D 14/15
X 69	<i>naviculus</i> (Hinde)	HOSIE 2 A
X 70	? sp. nov. A	ZLA 32
X 71	<i>Clydagnathus cavusformis</i> gen. et. sp. nov.	KL 7
X 72	<i>cavusiformis</i> gen. et. sp. nov.	KL 2
X 73	<i>cavusiformis</i> gen. et. sp. nov.	KL 5
X 74	<i>cavusiformis</i> gen. et. sp. nov.	KL 5
X 75	<i>cavusiformis</i> gen. et. sp. nov.	KL 5
X 76	<i>darensis</i> gen. et. sp. nov.	ZLA 13
X 77	<i>darensis</i> gen. et. sp. nov.	ZLA 27
X 78	<i>gilwernensis</i> gen. et. sp. nov.	KL 1
X 79	<i>unicornis</i> gen. et. sp. nov.	ZLA 14
X 80	<i>unicornis</i> gen. et. sp. nov.	ZLA 14
X 81	<i>unicornis</i> gen. et. sp. nov.	ZLA 11
X 82	gen. et. sp. nov. A	KL 13
X 83	<i>Euprioniodina caverna</i> (Collinson & Druce)	3D 14/15
X 84	<i>microdentata</i> (Ellison)	GILM 2
X 85	sp.	K 14
X 86	sp. nov. A	HOSIE 2 B
X 87	<i>Gnathodus delicatus</i> Branson & Mehl	ZLA 6
X 88	<i>simplicatus</i> sp. nov.	Z 38
X 89	<i>simplicatus</i> sp. nov.	ZLA 33
X 90	<i>simplicatus</i> sp. nov.	ZLA 33
X 91	<i>simplicatus</i> sp. nov.	ZLA 33
X 92	<i>Gnathodus</i> ? sp. nov.	ZL 8
X 93	<i>bilineatus</i> (Roundy)	3D 14/15
X 94	<i>bilineatus</i> (Roundy)	3D 14/15
X 95	<i>commutatus</i> . Branson & Mehl	3D 14/15
X 96	<i>commutatus</i> . Branson & Mehl	3D 14/15
X 97	<i>commutatus</i> . Branson & Mehl	3D 12
X 98	<i>cuneiformis</i> . Mehl & Thomas	S 11
X 99	<i>girtyi collinsoni</i> subsp. nov.	3D 14/15
X 100	<i>girtyi collinsoni</i> subsp. nov.	3D 14/15
X 101	<i>girtyi collinsoni</i> subsp. nov.	3D 14/15
X 102	<i>girtyi collinsoni</i> subsp. nov.	3D 14/15
X 103	<i>girtyi girtyi</i> Hass	HOSIE 2 A
X 104	<i>girtyi girtyi</i> Hass	HOSIE 2 A
X 105	<i>girtyi girtyi</i> Hass	HOSIE 2 A
X 106	<i>girtyi girtyi</i> Hass	HOSIE 2 A
X 107	<i>girtyi simplex</i> Dunn	HOSIE 2 A (1)
X 108	<i>girtyi simplex</i> Dunn	HOSIE 2 A 5
X 109	<i>Ozarkodina</i> cf. <i>elegans</i> (Stauffer)	Z 19

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 110	<i>Gnathodus girtyi simplex</i> Dunn	HOSIE 2 A
X 111	<i>girtyi simplex</i> Dunn	HOSIE 2 A
X 112	<i>girtyi soniae</i> subsp. nov.	3D 8
X 113	<i>girtyi soniae</i> subsp. nov.	3D 12
X 114	<i>girtyi soniae</i> subsp. nov.	3D 14/15
X 115	<i>girtyi soniae</i> subsp. nov.	3D 14/15
X 116	<i>girtyi turritus</i> Collinson & Druce	3D 23
X 117	<i>girtyi</i> subsp. nov.	CYD 7 A
X 118	<i>girtyi</i> subsp. nov.	CYD 7 A
X 119	<i>girtyi</i> subsp. nov.	CYD 7 A
X 120	<i>homopunctatus</i> Ziegler	3D 14/15
X 121	<i>homopunctatus</i> Ziegler	3D 14/15
X 122	<i>homopunctatus</i> Ziegler	3D 14/15
X 123	<i>homopunctatus</i> Ziegler	3D 14/15
X 124	<i>mononodosus</i> sp. nov.	3D 14/15
X 125	<i>mononodosus</i> sp. nov.	3D 14/15
X 126	<i>mononodosus</i> sp. nov.	3D 14/15
X 127	<i>nodosus</i> Bischoff	3D 14/15
X 128	<i>nodosus</i> Bischoff	3D 14/15
X 129	<i>nodosus</i> Bischoff	HOSIE 2 B
X 130	<i>Polygnathus</i> sp.	(SL 461) D 22
X 131	<i>Gnathodus punctatus</i> (Cooper)	Z 38
X 132	<i>punctatus</i> (Cooper)	Z 38
X 133	<i>punctatus</i> (Cooper)	Z 38
X 134	<i>symmutatus</i> sp. nov.	3D 10
X 135	<i>symmutatus</i> sp. nov.	3D 10
X 136	<i>symmutatus</i> sp. nov.	3D 14/15
X 137	<i>symmutatus</i> sp. nov.	3D 14/15
X 138	sp.	HOSIE 2 A
X 139	<i>Hibbardella (Hibbardella) acuta</i> Murray & Chronic	3D 14/15
X 140	<i>(Hibbardella) milleri</i> Rexroad	HOSIE 2 A
X 141	<i>(Hibbardella) milleri</i> Rexroad	HOSIE 2 B
X 142	<i>(Hibbardella) milleri</i> Rexroad	HOSIE 2 C
X 143	<i>(Hibbardella) ortha</i> Rexroad	HOSIE 2 A
X 144	<i>(Hibbardella) parva</i> sp. nov.	3D 14/15
X 145	<i>(Hibbardella) parva</i> sp. nov.	3D 14/15
X 146	<i>(Hibbardella)</i> cf. <i>macrodentata</i> Thomas	ZLA 32
X 147	<i>(Hibbardella)</i> cf. <i>macrodentata</i> Thomas	ZLA 32
X 148	<i>(Hibbardella)</i> cf. <i>macrodentata</i> Thomas	KL 3
X 149	<i>(Hassognathus) separata</i> (Branson & Mehl)	ZLA 6
X 150	<i>(Hassognathus) separata</i> (Branson & Mehl)	ZLA 7
X 151	<i>(Roundya) barnettana</i> Hass	3D 14/15
X 152	<i>(Roundya) barnettana</i> Hass	3D 14/15
X 153	<i>(Roundya) barnettana</i> Hass	HOSIE 3D 23
X 154	<i>(Roundya) barnettana</i> Hass	HOSIE 2 C
X 155	<i>Pseudopolygnathus vogesi</i> sp. nov.	K 12
X 156	<i>Hindeodella antecomplex</i> Collinson & Druce	3D 14/15
X 157	<i>antecomplex</i> Collinson & Druce	3D 17
X 158	<i>cooperi</i> (Elias)	3D 14/15
X 159	<i>cooperi</i> (Elias)	3D 14/15

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 160	<i>corpulenta</i> Branson & Mehl	KL 3
X 161	<i>corpulenta</i> Branson & Mehl	KL 19
X 162	<i>croka</i> Collinson & Druce	3D 14/15
X 163	<i>croka</i> Collinson & Druce	3D 14/15
X 164	<i>croka</i> Collinson & Druce	GILM 5
X 165	<i>croka</i> Collinson & Druce	3D 14/15
X 166	<i>Spathognathodus costatus costatus</i> (E. R. Branson)	ZLA 6
X 167	<i>hibbardi</i> Collinson & Druce	3D 14/15 3
X 168	<i>hibbardi</i> Collinson & Druce	3D 14/15 5
X 169	<i>hibbardi</i> Collinson & Druce	3D 14/15 6
X 170	<i>ibergensis</i> Bischoff	3D 14/15
X 171	<i>ibergensis</i> Bischoff	3D 14/15
X 172	<i>ibergensis</i> Bischoff	3D 14/15
X 173	<i>ibergensis</i> Bischoff	HOSIE 2 A
X 174	<i>ibergensis</i> Bischoff	GILM 2
X 175	<i>montanaensis</i> (Scott)	3D 12
X 176	<i>montanaensis</i> (Scott)	3D 12
X 177	<i>subtilis</i> Ulrich & Bassler	ZLA 33
X 178	<i>subtilis</i> Ulrich & Bassler	ZLA 33
X 179	<i>subtilis</i> Ulrich & Bassler	ZLA 33
X 180	<i>subtilis</i> Ulrich & Bassler	ZLA 14
X 181	<i>secarata</i> Collinson & Druce	ZLA 3D 14/15
X 182	<i>secarata</i> Collinson & Druce	ZLA 3D 14/15
X 183	<i>secarata</i> Collinson & Druce	ZLA 3D 14/15
X 184	<i>secarata</i> Collinson & Druce	CYD 7 A
X 185	<i>undata</i> Branson & Mehl	3D 14/15
X 186	sp. nov.	3D 14/15
X 187	<i>tenuis</i> Clarke	GILM 5
X 188	<i>Hindeodus</i> sp.	HOSIE 2 A
X 189	sp.	HOSIE 2 A
X 190	sp.	HOSIE 2 A
X 191	sp.	HOSIE 2 A
X 192	<i>alatoides</i> (Rexroad & Burton)	HOSIE 2 B
X 193	<i>alatoides</i> (Rexroad & Burton)	HOSIE 2 C
X 194	<i>imperfectus</i> (Rexroad)	HOSIE 2 B
X 195	<i>Kladognathus clavensis</i> Collinson & Druce	3D 10
X 196	<i>clavensis</i> Collinson & Druce	3D 10
X 197	<i>macrodentatus</i> (Higgins)	3D 14/15
X 198	<i>macrodentatus</i> (Higgins)	3D 14/15
X 199	<i>macrodentatus</i> (Higgins)	3D 14/15
X 200	<i>macrodentatus</i> (Higgins)	DUN 54
X 201	<i>Ligonodina beata</i> nom. nov.	KL 19
X 202	<i>beata</i> nom. nov.	ZLA 12
X 203	<i>beata</i> nom. nov.	ZLA 12
X 204	<i>levis</i> Branson & Mehl	HOSIE 2 A
X 205	<i>levis</i> Branson & Mehl	HOSIE 2 A
X 206	<i>levis</i> Branson & Mehl	HOSIE 2 B
X 207	<i>levis</i> Branson & Mehl	HOSIE 2 B
X 208	<i>magnilaterina</i> sp. nov.	HOSIE 2 C
X 209	<i>magnilaterina</i> sp. nov.	HOSIE 2 C

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 210	<i>magnilaterina</i> sp. nov.	HOSIE 2 C
X 211	<i>magnilaterina</i> sp. nov.	HOSIE 2 C
X 212	<i>osborni</i> sp. nov.	3D 14/15
X 213	<i>osborni</i> sp. nov.	3D 14/15
X 214	<i>roundyi</i> Hass	DUN 54
X 215	<i>roundyi</i> Hass	3D 14/15
X 217	sp. A	ZLA 32
X 218	? sp.	ZLA 11
X 219	? sp.	3D 10
X 220	<i>Apatognathus porcatus</i> (Hinde)	DUN 58
X 221	<i>Spathognathodus cyrius</i> (Cooper)	KL 16
X 222	<i>Lonchodina bolbosa</i> Collinson & Druce	3D 14/15
X 223	<i>bolbosa</i> Collinson & Druce	3D 14/15
X 224	<i>bolbosa</i> Collinson & Druce	3D 14/15
X 225	<i>furnishi</i> Rexroad	HOSIE 2 C
X 226	<i>furnishi</i> Rexroad	HOSIE 2 C
X 227	<i>furnishi</i> Rexroad	DUN 54
X 228	<i>furnishi</i> Rexroad	GILM 3
X 229	<i>obtunda</i> Collinson & Druce	3D 14/15
X 231	<i>paraclarki</i> Hass	3D 14/15
X 232	<i>paraclaviger</i> Rexroad	3D 14/15
X 233	<i>paraclaviger</i> Rexroad	3D 14/15
X 234	<i>transitans</i> Collinson & Druce	3D 14/15
X 235	<i>transitans</i> Collinson & Druce	3D 14/15
X 236	<i>transitans</i> Collinson & Druce	3D 10
X 237	<i>Magnilaterella complectens</i> (Clarke)	HOSIE 2 B
X 238	<i>complectens</i> (Clarke)	HOSIE 2 B
X 239	<i>complectens</i> (Clarke)	HOSIE 2 B
X 240	<i>complectens</i> (Clarke)	HOSIE 2 A
X 241	<i>clarkei</i> sp. nov.	BIL 102
X 242	spp.	HOSIE 2 A
X 243	sp.	DUN 76
X 244	sp.	GILM 2
X 245	<i>Mestognathus beckmanni</i> Bischoff	SCC 29
X 246	<i>bipluti</i> Higgins	ANS 15
X 247	<i>bipluti</i> Higgins	ANS 15
X 248	<i>bipluti</i> Higgins	CYD 7 A
X 249	<i>bipluti</i> Higgins	CYD 6 A
X 250	<i>neddensis</i> sp. nov.	CYD 6 A
X 251	<i>neddensis</i> sp. nov.	CYD 6 A
X 252	<i>neddensis</i> sp. nov.	CYD 7 A
X 253	<i>Metalonchodina bidentata</i> (Gunnell)	3D 14/15
X 254	<i>bidentata</i> (Gunnell)	3D 14/15
X 255	<i>bidentata</i> (Gunnell)	3D 14/15
X 256	<i>bidentata</i> (Gunnell)	BIL 102
X 257	<i>Neoprioniodus antespathatus</i> Collinson & Druce	3D 14/15
X 258	<i>antespathatus</i> Collinson & Druce	3D 14/15
X 259	<i>barbatus</i> (Branson & Mehl)	ZLA 11
X 260	<i>barbatus</i> (Branson & Mehl)	ZLA 11
X 261	<i>barbatus</i> (Branson & Mehl)	ZLA 13

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 262	<i>barbatus</i> (Branson & Mehl)	ZLA 14
X 263	<i>confluens</i> (Branson & Mehl)	ZLA 14
X 264	<i>confluens</i> (Branson & Mehl)	ZLA 33
X 265	<i>conjunctus</i> (Gunnell)	HOSIE 2 B
X 266	<i>conjunctus</i> (Gunnell)	HOSIE 2 B
X 267	<i>conjunctus</i> (Gunnell)	HOSIE 2 C
X 268	<i>montanaensis</i> (Scott)	3D 14/15
X 269	<i>montanaensis</i> (Scott)	3D 14/15
X 270	<i>montanaensis</i> (Scott)	3D 14/15
X 271	<i>montanaensis</i> (Scott)	3D 14/15
X 272	<i>peracutus</i> (Hinde)	3D 14/15
X 273	<i>peracutus</i> (Hinde)	3D 14/15
X 274	<i>peracutus</i> (Hinde)	3D 14/15
X 275	<i>peracutus</i> (Hinde)	3D 14/15
X 276	<i>scitulus</i> (Branson & Mehl)	HOSIE 2 A
X 277	<i>scitulus</i> (Branson & Mehl)	HOSIE 2 A
X 278	<i>scitulus</i> (Branson & Mehl)	HOSIE 2 B VI 36
X 279	<i>spathatus</i> Higgins	3D 14/15
X 280	<i>tulensis</i> (Pander)	DUN 54
X 281	<i>varians</i> (Branson & Mehl)	3D 14/15
X 282	sp. nov. A	3D 17
X 283	cf. <i>armatus</i> (Hinde)	ZLA 14
X 284	cf. <i>camurus</i> Rexroad	VEX 1
X 285	cf. <i>camurus</i> Rexroad	VEX 1
X 286	cf. <i>camurus</i> Rexroad	GILM 1
X 287	cf. <i>camurus</i> Rextoad	HOSIE 2 C
X 288	<i>Ozarkodina</i> cf. <i>congesta</i> Stauffer	Z 37
X 289	<i>curvata</i> Rexroad	GILM 3
X 290	<i>delicatula</i> (Stauffer & Plummer)	3D 4
X 291	<i>delicatula</i> (Stauffer & Plummer)	3D 14/15
X 292	<i>delicatula</i> (Stauffer & Plummer)	ZLA 31
X 293	<i>hindei</i> Clarke	HOSIE 2 B
X 294	<i>hindei</i> Clarke	HOSIE 2 A
X 295	<i>hindei</i> Clarke	GILM 5
X 296	<i>macra</i> Branson & Mehl	K 4
X 297	<i>macra</i> Branson & Mehl	K 22
X 298	<i>macra</i> Branson & Mehl	Z 18
X 299	<i>parva</i> (Huddle)	C 7
X 300	<i>plana</i> (Huddle)	K 3
X 301	<i>plana</i> (Huddle)	K 13
X 302	<i>plumula</i> Collinson & Druce	3D 12
X 303	<i>plumula</i> Collinson & Druce	3D 12
X 304	<i>macer</i> (Branson & Mehl)	Z 35
X 305	<i>macer</i> (Branson & Mehl)	Z 38
X 306	sp.	C 7
X 307	sp.	K 13
X 308	sp.	Z 16
X 309	<i>Patrognathus variabilis</i> gen. et. sp. nov.	KL 2
X 310	<i>variabilis</i> gen. et. sp. nov.	KL 2
X 311	<i>variabilis</i> gen. et. sp. nov.	KL 2

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 312	<i>Plectospathodus</i> ? sp. nov. A	ZLA 33
X 313	sp. nov. A	ZLA 33
X 314	sp. nov. B	3D 17
X 315	<i>Prioniodina eireica</i> (Collinson & Druce)	3D 17
X 316	<i>laevipostica</i> (Rexroad & Collinson)	CYD 7 A
X 317	<i>laevipostica</i> (Rexroad & Collinson)	CYD 7 A
X 318	<i>Apatognathus</i> sp.	HOSIE 2A
X 319	<i>Hibbardella</i> (<i>Hassognathus</i>) sp.	DUN 77
X 320	<i>Ligonodina tenuis</i> Branson & Mehl	3D 22
X 321	<i>tenuis</i> Branson & Mehl	3D 22
X 322	<i>Magnilaterella</i> spp.	3D 14/15
X 323	spp.	3D 14/15
X 324	<i>Hindeodella undata</i> Branson & Mehl	3D 14/15 (not figured)
X 325	<i>Ozarkodina hindei</i> Clarke	3D 12 (not figured)
X 326	<i>Apatognathus porcatus</i> (Hinde)	HOSIE 2C (not figured)
X 392	<i>Cavusgnathus unicornis</i> Youngquist & Miller	S 49
X 327	<i>Geniculatus</i> sp.	DUN 59
X 328	<i>Ligonodina tulensis</i> (Pander)	CYD 3
X 330	<i>Prioniodina oweni</i> sp. nov.	ZLA 5
X 331	<i>prelaevipostica</i> sp. nov.	ZLA 11
X 332	<i>prelaevipostica</i> sp. nov.	ZLA 11
X 333	<i>prelaevipostica</i> sp. nov.	ZLA 6
X 334	<i>prelaevipostica</i> sp. nov.	ZLA 33
X 335	<i>prelaevipostica</i> sp. nov.	ZLA 33
X 336	<i>prelaevipostica</i> sp. nov.	ZLA 33
X 337	<i>stipans</i> (Rexroad)	3D 14/15
X 338	<i>stipans</i> (Rexroad)	3D 14/15
X 339	<i>stipans</i> (Rexroad)	3D 14/15
X 340	<i>stipans</i> (Rexroad)	3D 14/15
X 341	<i>subaequalis</i> (Higgins)	3D 14/15
X 342	<i>subaequalis</i> (Higgins)	3D 14/15
X 343	<i>subaequalis</i> (Higgins)	3D 14/15
X 344	<i>subaequalis</i> (Higgins)	3D 14/15
X 345	? sp. nov.	GILM 3
X 346	<i>Polygnathus communis communis</i> Branson & Mehl	ZLA 14
X 347	<i>communis communis</i> Branson & Mehl	ZLA 14
X 348	<i>communis communis</i> Branson & Mehl	ZLA 14
X 349	<i>bischoffi</i> sp. nov.	SCC
X 350	<i>bischoffi</i> sp. nov.	SCC
X 351	<i>bischoffi</i> sp. nov.	SCC
X 352	<i>bischoffi</i> sp. nov.	C 20
X 353	<i>inornatus inornatus</i> Branson & Mehl	KLM 1
X 354	<i>inornatus inornatus</i> Branson & Mehl	KLM 1
X 355	<i>inornatus inornatus</i> Branson & Mehl	KL 19
X 356	<i>inornatus rostratus</i> subsp. nov.	KL 19
X 357	<i>inornatus rostratus</i> subsp. nov.	KL 19
X 358	<i>inornatus vexatus</i> subsp. nov.	KL 19
X 359	<i>inornatus vexatus</i> subsp. nov.	KLM 1
X 360	<i>lacinatus asymmetricus</i> subsp. nov.	ZLA 33
X 361	<i>lacinatus asymmetricus</i> subsp. nov.	ZLA 32

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 362	<i>lacinatus asymmetricus</i> subsp. nov.	ZLA 32
X 363	<i>lacinatus asymmetricus</i> subsp. nov.	ZLA 31
X 364	<i>lacinatus circaperipherus</i> subsp. nov.	ZLA 32
X 365	<i>lacinatus circaperipherus</i> subsp. nov.	ZLA 32
X 366	<i>lacinatus circaperipherus</i> subsp. nov.	ZLA 32
X 367	<i>lacinatus circaperipherus</i> subsp. nov.	ZLA 32
X 368	<i>lacinatus lacinatus</i> Huddle	ZLA 31
X 369	<i>lacinatus lacinatus</i> Huddle	ZLA 31
X 370	<i>lacinatus lacinatus</i> Huddle	ZLA 31
X 371	<i>lacinatus prelobatus</i> subsp. nov.	ZLA 32
X 372	<i>lacinatus prelobatus</i> subsp. nov.	ZLA 32
X 373	<i>lacinatus prelobatus</i> subsp. nov.	ZLA 32
X 374	<i>lacinatus prelobatus</i> subsp. nov.	ZLA 32
X 372	<i>lacinatus prelobatus</i> subsp. nov.	ZLA 32
X 375	<i>lobatus inflexus</i> subsp. nov.	KLM 1
X 376	<i>lobatus lobatus</i> Branson & Mehl	KLM 1
X 377	<i>lobatus lobatus</i> Branson & Mehl	KL 19
X 378	<i>lobatus lobatus</i> Branson & Mehl	KL 19
X 379	<i>Spathognathodus plumulus plumulus</i> sp. et. subsp. nov.	KL 7
X 380	<i>plumulus plumulus</i> sp. et. subsp. nov.	KL2 11
X 381	<i>plumulus plumulus</i> sp. et. subsp. nov.	KL2 11
X 382	<i>plumulus nodosus</i> subsp. nov.	KL 1
X 383	<i>plumulus nodosus</i> subsp. nov.	KL 1
X 384	<i>plumulus shirleyae</i> subsp. nov.	KL 2
X 385	<i>plumulus shirleyae</i> subsp. nov.	KL 3
X 386	<i>pulcher</i> (Branson & Mehl)	ZLA 31
X 387	cf. <i>robustus</i> (Branson & Mehl)	ZLA 10
X 388	cf. <i>robustus</i> (Branson & Mehl)	ZLA 10
X 389	<i>scitulus</i> (Hinde)	DUN 78
X 390	<i>scitulus</i> (Hinde) subsp. nov. A	DUN 78
X 391	<i>scitulus</i> (Hinde)	GILM 1
X 392	<i>scitulus</i> (Hinde)	HOSIE 2 A
X 393	<i>scitulus</i> (Hinde)	CYD 7 A
X 394	<i>tridentatus</i> (E. R. Branson)	ZLA 14
X 395	<i>tridentatus</i> (E. R. Branson)	ZLA 14
X 396	<i>tridentatus</i> (E. R. Branson)	ZL 8
X 397	<i>tridentatus</i> (E. R. Branson)	KL 19
X 398	<i>bischoffi</i> sp. nov.	GUD 3
X 399	<i>bischoffi</i> sp. nov.	GUD 8
X 400	<i>bischoffi</i> sp. nov.	GUD 4
X 401	<i>bischoffi</i> sp. nov.	GUD 5
X 402	<i>zieglerei</i> sp. nov.	GUD 2
X 403	<i>zieglerei</i> sp. nov.	GUD 9
X 404	<i>zieglerei</i> sp. nov.	GUD 10
X 405	sp. A	KL 3 V
X 406	sp. B	ZLA 5
X 407	<i>Taphrognathus varians</i> Branson & Mehl	HAR 20
X 408	<i>varians</i> Branson & Mehl	HAR 16
X 409	Gen. nov. A. sp.	ZLA 6
X 410	Gen. nov. B. sp.	ORZ 1

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 411	<i>Gnathodus avonensis</i> sp. nov.	Z 38
X 412	<i>antetexanus</i> Rexroad & Scott	ZLA 32
X 413	<i>antetexanus</i> Rexroad & Scott	ZLA 33
X 414	<i>antetexanus</i> Rexroad & Scott	C 4
X 415	<i>simplicatus</i> sp. nov.	ZLA 32
X 416	<i>bilineatus</i> (Roundy)	3D 14/15
X 417	<i>bilineatus</i> (Roundy)	3D 14/15
X 418	<i>commutatus</i> (Branson & Mehl)	3D 14/15
X 419	<i>Ozarkodina plana</i> (Huddle)	K 3
X 420	<i>compressa</i> Rexroad	3D 22A
X 421	<i>Gnathodus semiglaber</i> Bischoff	Z 30
X 422	<i>Hibbardella acuta</i> Murray & Chronic	3D 14/15
X 423	sp.	ZLA 32
X 424	<i>Lonchodina</i> sp. A	ZLA 32
X 425	<i>Gnathodus</i> sp.	HOSIE 2 A
X 426	<i>delicatus</i> Branson & Mehl	Z 32
X 427	<i>Plectospathodus</i> ? sp. nov. B	3D 14/15
X 428	sp. nov. B	3D 14/15
X 429	<i>Prioniodina latericrescens</i> (Branson & Mehl)	Z 22
X 430	<i>Polygnathus P. communis communis</i> Branson & Mehl	KLM 1
X 431	<i>Magnilaterella clarkei</i> sp. nov.	BIL 102
X 432	<i>clarkei</i> sp. nov.	DUN 54
X 433	<i>Pseudopolygnathus longiposticus</i> Branson & Mehl	Z 38
X 434	<i>longiposticus</i> Branson & Mehl	Z 38
X 435	<i>Spathognathodus</i> cf. <i>campbelli</i> Rexroad	3D 14/15
X 436	<i>coaptus</i> (Branson & Mehl)	Z 36
X 437	<i>ziegleri</i> sp. nov.	GUD 7
X 438	<i>Pseudopolygnathus dentilineatus</i> E. R. Branson	Z 17
X 439	<i>Gnathodus bilineatus bilineatus</i> (Roundy)	3D 14/15
X 440	<i>Polygnathus lobatus lobatus</i> Branson & Mehl	KL 19
X 441	<i>Hibbardella</i> (<i>Hibbardella</i>) sp.	KL 16
X 442	<i>Pseudopolygnathus</i> cf. <i>longiposticus</i> Branson & Mehl	Z 38
X 443	cf. <i>longiposticus</i> Branson & Mehl	Z 38
X 444	<i>longiposticus</i> Branson & Mehl	Z 38
X 445	<i>longiposticus</i> Branson & Mehl	Z 38
X 446	<i>Hindeodella</i> sp.	ZLA 33
X 447	<i>Magnilaterella</i> ? sp.	ZLA 37
X 448	<i>Pseudopolygnathus</i> cf. <i>longiposticus</i> Branson & Mehl	Z 38
X 449	cf. <i>longiposticus</i> Branson & Mehl	Z 38
X 450	<i>Spathognathodus</i> cf. <i>campbelli</i> Rexroad	3D 14/15
X 451	cf. <i>campbelli</i> Rexroad	3D 14/15
X 452	cf. <i>campbelli</i> Rexroad	3D 14/15
X 453	<i>coaptus</i> (Branson & Mehl)	Z 38
X 454	<i>coaptus</i> (Branson & Mehl)	Z 36
X 455	<i>costatus costatus</i> (E. R. Branson)	ZLA 6
X 456	<i>costatus costatus</i> (E. R. Branson)	ZLA 8
X 457	<i>costatus sulciferus</i> (Branson & Mehl)	ZLA 6
X 458	<i>costatus sulciferus</i> (Branson & Mehl)	ZLA 12
X 459	<i>costatus sulciferus</i> (Branson & Mehl)	ZLA 12
X 460	<i>crassidentatus</i> (Branson & Mehl)	ZLA 15

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 461	<i>crassidentatus</i> (Branson & Mehl)	ZLA 15
X 462	<i>crassidentatus</i> (Branson & Mehl)	ZLA 15
X 463	<i>crassidentatus</i> (Branson & Mehl)	ZLA 15
X 464	<i>cristulus</i> Youngquist & Miller	HOSIE 2 A
X 465	<i>cristulus</i> Youngquist & Miller	HOSIE 2 A
X 466	<i>cristulus</i> Youngquist & Miller	HOSIE 2 B
X 467	<i>cristulus</i> Youngquist & Miller	VEX 1
X 468	<i>cristulus</i> Youngquist & Miller	GILM 1
X 469	cf. <i>cyrius</i> (Cooper)	KL 19
X 470	cf. <i>cyrius</i> (Cooper)	KL 16
X 471	cf. <i>cyrius</i> (Cooper)	KLM 1
X 472	<i>elongatus</i> (Branson & Mehl)	KL 20
X 473	<i>elongatus</i> (Branson & Mehl)	ZLA 6
X 474	<i>elongatus</i> (Branson & Mehl)	ZLA 10
X 475	<i>elongatus</i> (Branson & Mehl)	ZL 8
X 476	<i>plumulus plumulus</i> sp. nov.	KL 4
X 477	<i>Pseudopolygnathus dentilineatus</i> E. R. Branson	Z 17
X 478	<i>dentilineatus</i> E. R. Branson	Z 16
X 479	<i>dentilineatus</i> E. R. Branson	Z 16
X 480	<i>dentilineatus</i> E. R. Branson	Z 16
X 481	<i>dentilineatus</i> E. R. Branson	Z 16
X 482	<i>expansus</i> sp. nov.	K 12
X 483	<i>expansus</i> sp. nov.	K 12
X 484	<i>multistriatus</i> Mehl & Thomas	ZLA 33
X 485	<i>multistriatus</i> Mehl & Thomas	Z 26
X 486	<i>multistriatus</i> Mehl & Thomas	Z 26
X 487	<i>multistriatus</i> Mehl & Thomas	Z 26
X 488	<i>nodomarginatus</i> (E. R. Branson)	ZLA 31
X 489	<i>nodomarginatus</i> (E. R. Branson)	ZLA 31
X 490	<i>nodomarginatus</i> (E. R. Branson)	ZLA 31
X 491	<i>nodomarginatus</i> (E. R. Branson)	ZLA 31
X 492	<i>nodomarginatus</i> (E. R. Branson)	ZLA 32
X 493	<i>nodomarginatus</i> (E. R. Branson)	ZLA 32
X 494	<i>nodomarginatus</i> (E. R. Branson)	ZLA 32
X 495	<i>nodomarginatus</i> (E. R. Branson)	ZLA 32
X 496	<i>postinodosus</i> sp. nov.	Z 38
X 497	<i>primus</i> Branson & Mehl	Z 17
X 498	<i>primus</i> Branson & Mehl	Z 17
X 499	<i>primus</i> Branson & Mehl	Z 22
X 500	<i>primus</i> Branson & Mehl	Z 17
X 501	<i>vogesi</i> sp. nov.	KL 2
X 502	<i>triangulus</i> cf. <i>pinnatus</i> Voges	C 7
X 503	<i>vogesi</i> sp. nov.	K 12
X 504	<i>vogesi</i> sp. nov.	K 12
X 505	<i>vogesi</i> sp. nov.	KL 12
X 506	<i>vogesi</i> sp. nov.	KL 2
X 507	<i>vogesi</i> sp. nov.	KL 9
X 508	<i>Hibbardella abnormis</i> Branson & Mehl	CYD 6
X 509	<i>Gnathodus nodosus</i> Bischoff	3D 14/15
X 510	<i>nodosus</i> Bischoff	3D 14/15

Slide Nos of figured specimens	Name of Conodont	Sample Number
X 511	<i>Magnilaterella</i> sp.	3D 12
X 512	<i>Spathognathodus pulcher</i> (Branson & Mehl)	Z 35
X 513	<i>pulcher</i> (Branson & Mehl)	Z 35
X 514	<i>Hindeodella brevis</i> Branson & Mehl	3D 14/15
X 515	<i>Pseudopolygnathus</i> sp. A	ZLA 31
X 516	<i>Polygnathus</i> cf. <i>communis</i> Branson & Mehl	KLM 140
X 517	<i>Magnilaterella contraria</i> sp. nov.	HOSIE 2 B
X 518	<i>Spathognathodus</i> sp. nov.	Z 20
X 519	<i>Patrognathus variabilis</i> gen. et. sp. nov.	KL 2
X 520	<i>Neoprioniodus</i> cf. <i>N. confluens</i> (Branson & Mehl)	KL 19
X 521	<i>Gnathodus punctatus</i> - <i>Gnathodus semiglaber</i> transition	Z 38
X 522	<i>Pseudopolygnathus</i> cf. <i>longiposticus</i> Branson & Mehl	Z 38
X 523	cf. <i>longiposticus</i> Branson & Mehl	Z 38
X 524	<i>Kladognathus mehli</i> (Rexroad)	3D 14/15
X 525	<i>Gnathodus punctatus</i> - <i>Gnathodus semiglaber</i> transition	Z 38
X 526	Gen. et. sp. indet.	ZLA 31
X 527	<i>Lonchodina furnishi</i> Rexroad	3D 23
X 528	<i>Magnilaterella robusta</i> Rexroad & Collinson	DUN 78
X 529	<i>robusta</i> Rexroad & Collinson	DUN 78
X 530	<i>Polygnathus inornatus rostratus</i> sub. sp. nov.	KL 4
X 531	sp.	FAR 4 A
X 532	<i>Scaphignathus</i> ? sp. A	ZL 2
X 533	sp. B	ZL 9
X 534	<i>Siphonodella isosticha</i> (Cooper)	KL 16
X 535	<i>isosticha</i> (Cooper)	KL 16
X 536	<i>obsoleta</i> Hass	KLM 1
X 537	sp. A	KL 16
X 538	sp.	K 12
X 539	sp.	K 17
X 540	<i>Spathognathodus anteposicornis</i> Scott	ZLA 15
X 541	<i>anteposicornis</i> Scott	ZLA 15
X 542	<i>anteposicornis</i> Scott	ZLA 14
X 543	<i>anteposicornis</i> Scott	KL 19
X 544	<i>Gnathodus antetexanus</i> Rexroad & Scott	C 7
X 545	<i>Pseudopolygnathus</i> cf. <i>longiposticus</i> Branson & Mehl	Z 38
X 546	<i>primus</i> Branson & Mehl	Z 17
X 547	<i>longiposticus</i> Branson & Mehl	Z 38
X 548	<i>Magnilaterella robusta</i> Rexroad & Collinson	DUN 78
X 549	<i>Pseudopolygnathus primus</i> Branson & Mehl	Z 18
X 550	<i>Apatognathus chauliodus</i> Varker	HOSIE 2B
X 551	<i>Polygnathus inornatus vexatus</i> sub. sp. nov.	KLM 1
X 552	<i>Pseudopolygnathus</i> cf. <i>fusiformis</i> Branson & Mehl	C 14
X 553	<i>Magnilaterella contraria</i> sp. nov.	ZLA 33
X 554	<i>Spathognathodus</i> cf. <i>cristulus</i> Youngquist & Miller	ZLA 33
X 555	cf. <i>cristulus</i> Youngquist & Miller	ZL 18
X 556	cf. <i>cristulus</i> Youngquist & Miller	ZLA 33
X 557	cf. <i>cristulus</i> Youngquist & Miller	ZLA 33
X 558	<i>Taphrognathus</i> - <i>Cavusgnathus</i> transition	S 49
X 559	<i>Taphrognathus</i> - <i>Cavusgnathus</i> transition	S 49
X 560	<i>Taphrognathus</i> - <i>Cavusgnathus</i> transition	S 49

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PLATES

PLATE 1

All specimens coated and magnified $\times 31.5$

FIGS. 1, 2, 5, 6. *Spathognathodus plumulus plumulus* sp. nov.

1a. Outer lateral view of holotype X 476. 1b. Oral view of holotype X 476. 1c. Aboral view of holotype X 476. 2a. Outer lateral view of paratype X 379. 2b. Oral view of paratype X 379. 2c. Aboral view of paratype X 379. 5. Outer lateral view of paratype X 380, posterior portion missing. 6. Outer lateral view of juvenile paratype X 381, anterior aboral portion of blade missing.

FIGS. 3, 4. *Spathognathodus plumulus nodosus* subsp. nov.

3a. Outer lateral view of paratype X 383, posterior portion missing. 3b. Oral view of paratype X 383. 3c. Aboral view of paratype X 383. 4a. Outer lateral view of holotype X 382, posterior portion missing. 4b. Oral view of holotype X 382. 4c. Aboral view of holotype X 382.

FIGS. 7, 8. *Spathognathodus plumulus shirleyae* sp. et subsp. nov.

7a. Outer lateral view of paratype X 385, posterior portion missing. 7b. Oral view of paratype X 385. 8a. Outer lateral view of holotype X 384. 8b. Oral view of holotype X 384. 8c. Aboral view of holotype X 384.

FIGS. 9-13. *Clydagnathus cavusformis* gen. et sp. nov.

9. Oral view of paratype X 72. 10. Oral view of paratype X 73. 11a. Outer lateral view of holotype X 75. 11b. Inner lateral view of holotype X 75. 11c. Oral view of holotype X 75. 11d. Aboral view of holotype X 75. 12a. Outer lateral view of paratype X 71. 12b. Inner lateral view of paratype X 71. 12c. Oral view of paratype X 71. 12d. Aboral view of paratype X 71. 13a. Outer lateral view of paratype X 74, posterior portion missing. 13b. Inner lateral view of paratype X 74. 13c. Oral view of paratype X 74. 13d. Aboral view of paratype X 74.

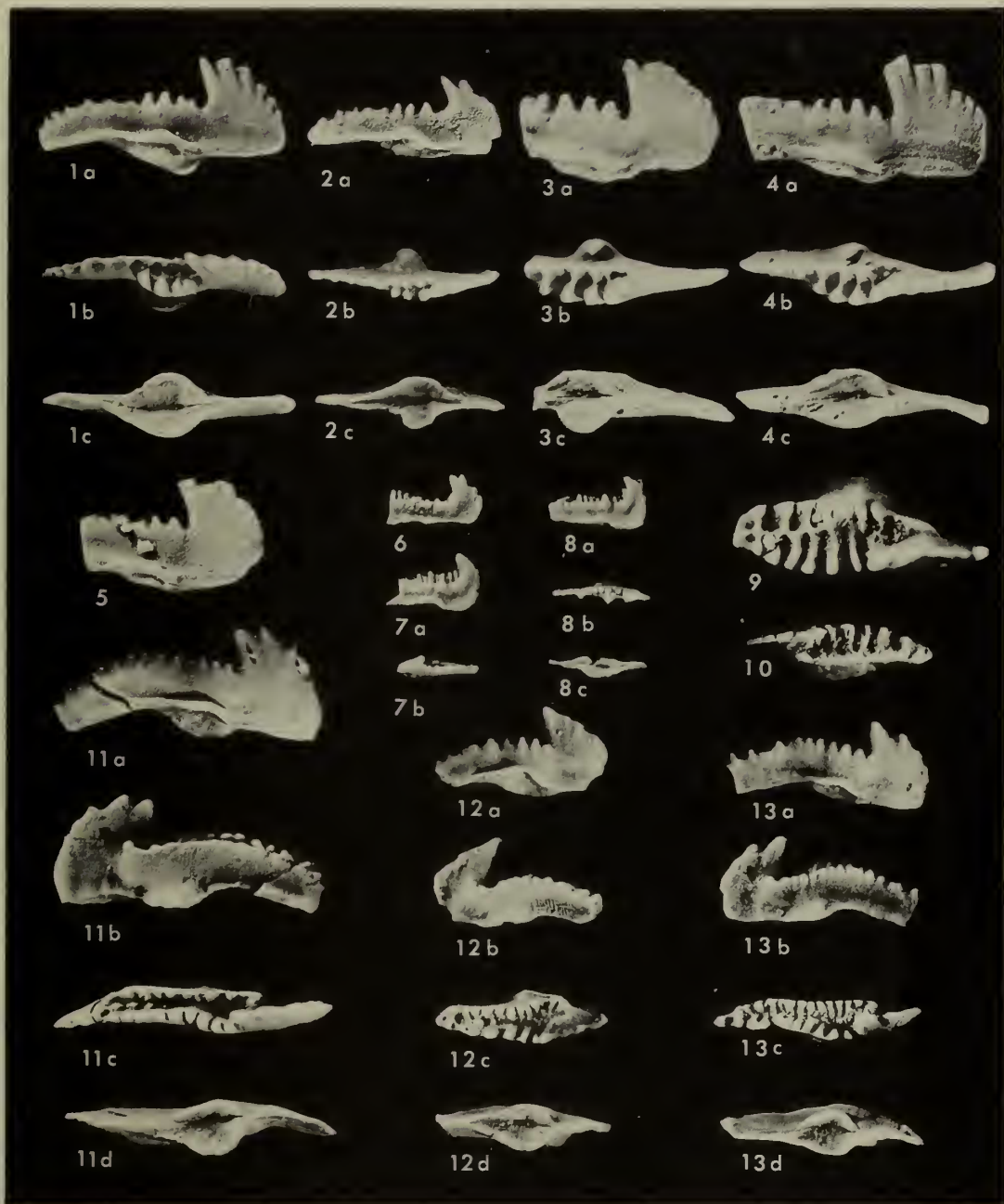


PLATE 2

All specimens coated and magnified $\times 31.5$

FIG. 1. *Clydagnathus gilwernensis* gen. et sp. nov.

a. Oral view of holotype X 78. b. Outer lateral view of holotype X 78. c. Inner lateral view of holotype X 78. d. Aboral view of holotype X 78.

FIGS. 2, 3, 5. *Clydagnathus unicornis* gen. et sp. nov.

2a. Oral view of holotype X 79. 2b. Outer lateral view of holotype X 79. 2c. Inner lateral view of holotype X 79. 2d. Aboral view of holotype X 79. 3a. Oral view of paratype X 80. 3b. Outer lateral view of paratype X 80. 3c. Inner lateral view of paratype X 80. 3d. Aboral view of paratype X 80. 5a. Oral view of paratype X 81. 5b. Inner lateral view of paratype X 81.

FIG. 4. *Clydagnathus* gen. et sp. nov. A

a. Oral view of specimen X 82. b. Outer lateral view of specimen X 82. c. Inner lateral view of specimen X 82. d. Aboral view of specimen X 82.

FIGS. 6, 7. *Clydagnathus darensis* gen. et sp. nov.

6a. Oral view of holotype X 77. 6b. Outer lateral view of holotype X 77. 6c. Inner lateral view of holotype X 77. 6d. Aboral view of holotype X 77. 7a. Oral view of paratype X 76. 7b. Outer lateral view of paratype X 76. 7c. Inner lateral view of paratype X 76. 7d. Aboral view of paratype X 76.

FIGS. 8-11. *Patrognathus variabilis* gen. et sp. nov.

8a. Oral view of paratype X 310. 8b. Lateral view of paratype X 310. 9a. Oral view of paratype X 519. 9b. Aboral view of paratype X 519. 9c. Lateral view of paratype X 519. 10a. Oral view of paratype X 309. 10b. Aboral view of paratype X 309. 10c. Lateral view of paratype X 309. 11a. Oral view of holotype X 311. 11b. Aboral view of holotype X 311. 11c. Lateral view of holotype X 311.

FIG. 12. *Scaphignathus* ? sp. B

a. Oral view of specimen X 533. b. Inner lateral view of specimen X 533. c. Aboral view of specimen X 533.

FIG. 13. *Scaphignathus* ? sp. A

a. Oral view of specimen X 532. b. Inner lateral view of specimen X 532. c. Aboral view of specimen X 532.

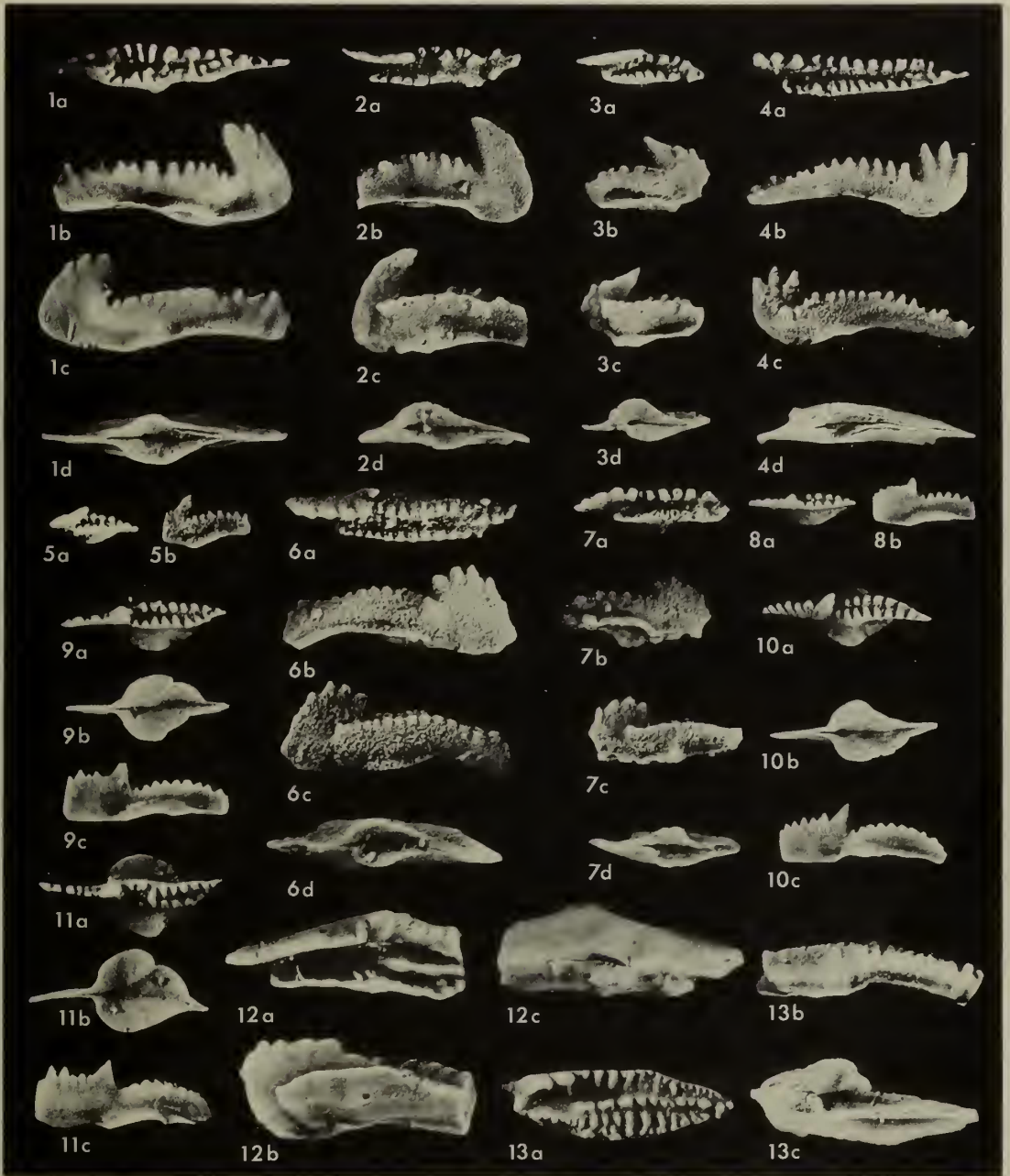


PLATE 3

All specimens coated and magnified $\times 31.5$

FIGS. 1-4. *Spathognathodus crassidentatus* (Branson & Mehl)

1a. Inner lateral view of specimen X 463. 1b. Aboral view of specimen X 463. 2a. Inner lateral view of specimen X 460. 2b. Oral view of specimen X 460. 3a. Inner lateral view of specimen X 461. 3b. Aboral view of specimen X 461. 4a. Inner lateral view of specimen X 462. 4b. Aboral view of specimen X 462.

FIGS. 5-8. *Spathognathodus anteposicornis* Scott

5a. Inner lateral view of specimen X 540. 5b. Oral view of specimen X 540. 6a. Inner lateral view of specimen X 543. 6b. Aboral view of specimen X 543. 7a. Inner lateral view of specimen X 541. 7b. Aboral view of specimen X 541. 8a. Inner lateral view of specimen X 542. 8b. Oral view of specimen X 542.

FIGS. 9-12. *Spathognathodus tridentatus* (E. R. Branson)

9a. Inner lateral view of specimen X 395. 9b. Oral view of specimen X 395. 9c. Aboral view of specimen X 395. 10a. Inner lateral view of specimen X 396. 10b. Oral view of specimen X 396. 10c. Aboral view of specimen X 396. 11a. Inner lateral view of specimen X 397. 11b. Oral view of specimen X 397. 11c. Aboral view of specimen X 397. 12a. Inner lateral view of specimen X 394. 12b. Oral view of specimen X 394. 12c. Aboral view of specimen X 394.

FIGS. 13-15. *Spathognathodus costatus costatus* (E. R. Branson)

13a. Inner lateral view of specimen X 456. 13b. Aboral view of specimen X 456. 14a. Inner lateral view of specimen X 166. 14b. Oral view of specimen X 166. 15a. Inner lateral view of specimen X 455. 15b. Oral view of specimen X 455.

FIGS. 16-18. *Spathognathodus costatus sulciferus* (Branson & Mehl)

16a. Inner lateral view of specimen X 459. 16b. Oral view of specimen X 459. 17a. Inner lateral view of specimen X 458. 17b. Aboral view of specimen X 458. 17c. Oral view of specimen X 458. 18a. Aboral view of specimen X 457. 18b. Inner lateral view of specimen X 457. 18c. Oral view of specimen X 457.

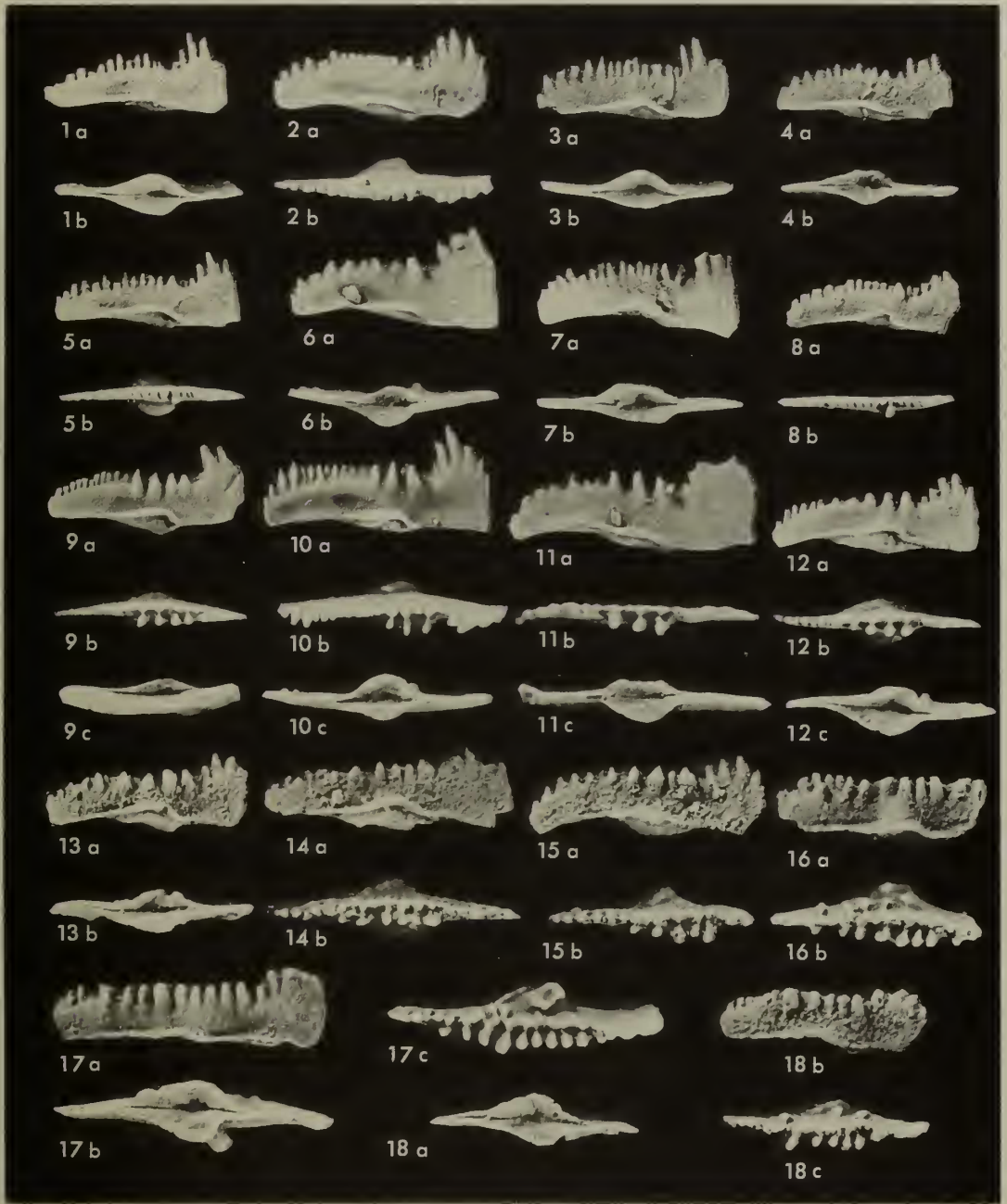


PLATE 4

All specimens coated and magnified $\times 31.5$

FIGS. 1-4. *Spathognathodus bischoffi* sp. nov.

1a. Oral view of paratype X 399. 1b. Aboral view of paratype X 399. 1c. Outer lateral view of paratype X 399. 1d. Inner lateral view of paratype X 399. 2a. Oral view of paratype X 400. 2b. Aboral view of paratype X 400. 2c. Outer lateral view of paratype X 400. 2d. Inner lateral view of paratype X 400. 3a. Oral view of paratype X 398. 3b. Aboral view of paratype X 398. 3c. Outer lateral view of paratype X 398. 3d. Inner lateral view of paratype X 398. 4a. Oral view of holotype X 401. 4b. Aboral view of holotype X 401. 4c. Outer lateral view of holotype X 401. 4d. Inner lateral view of holotype X 401.

FIGS. 5-8. *Spathognathodus zieglerei* sp. nov.

5a. Oral view of paratype X 437. 5b. Aboral view of paratype X 437. 5c. Outer lateral view of paratype X 437. 5d. Inner lateral view of paratype X 437. 6a. Oral view of paratype X 402. 6b. Aboral view of paratype X 402. 6c. Outer lateral view of paratype X 402. 6d. Inner lateral view of paratype X 402. 7a. Oral view of paratype X 404. 7b. Aboral view of paratype X 404. 7c. Outer lateral view of paratype X 404. 7d. Inner lateral view of paratype X 404. 8a. Oral view of holotype X 403. 8b. Aboral view of holotype X 403. 8c. Outer lateral view of holotype X 403. 8d. Inner lateral view of holotype X 403.

FIGS. 9-11. *Spathognathodus pulcher* Branson & Mehl

9a. Oral view of specimen X 386. 9b. Aboral view of specimen X 386. 9c. Lateral view of specimen X 386. 10a. Oral view of specimen X 513. 10b. Aboral view of specimen X 513. 10c. Lateral view of specimen X 513. 11a. Oral view of specimen X 512. 11b. Aboral view of specimen X 512. 11c. Lateral view of specimen X 512.

FIG. 12. *Spathognathodus* sp. A

a. Oral view of specimen X 405. b. Aboral view of specimen X 405. c. Lateral view of specimen X 405.

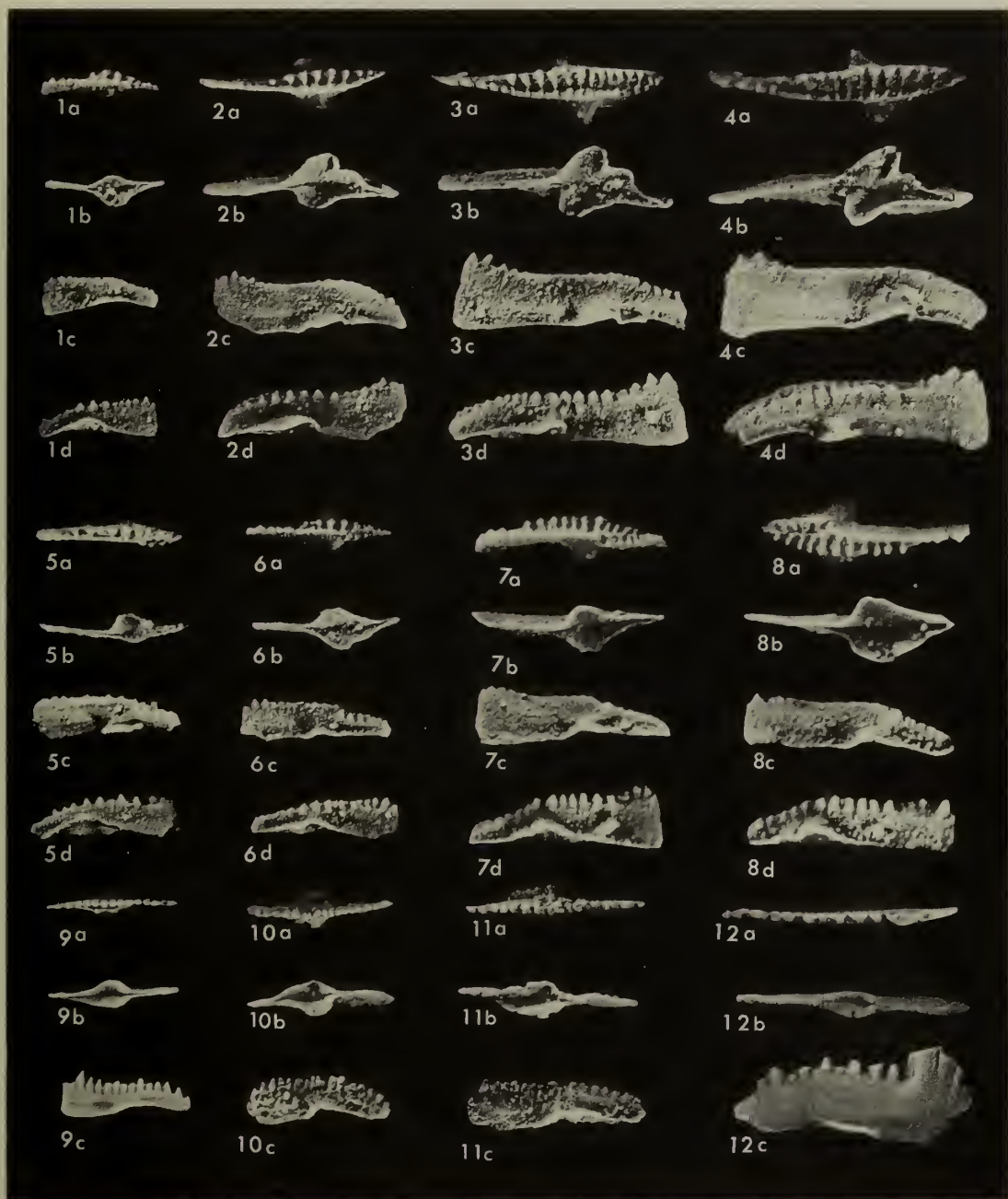


PLATE 5

All specimens coated and magnified $\times 31.5$

FIGS. 1, 3, 5-8. *Pseudopolygnathus vogesi* sp. nov.

1a. Aboral view of holotype X 155. 1b. Oral view of holotype X 155. 1c. Lateral view of holotype X 155. 3a. Aboral view of paratype X 504. 3b. Oral view of paratype X 504. 3c. Lateral view of paratype X 504. 5a. Oral view of paratype X 507. 5b. Aboral view of paratype X 507. 5c. Lateral view of paratype X 507. 6a. Oral view of paratype X 505. transitional to *Ps. expansus*. 6b. Aboral view of paratype X 505. 6c. Lateral view of paratype X 505. 7a. Aboral view of paratype X 501. 7b. Oral view of paratype X 501. 8a. Aboral view of paratype X 506. 8b. Oral view of paratype X 506.

FIGS. 2, 4. *Pseudopolygnathus expansus* sp. nov.

2a. Aboral view of paratype X 482. 2b. Oral view of paratype X 482. 2c. Lateral view of paratype X 482. 4a. Oral view of holotype X 483. 4b. Aboral view of holotype X 483. 4c. Lateral view of holotype X 483.

FIGS. 9-13. *Pseudopolygnathus dentilineatus* E. R. Branson

9a. Aboral view of juvenile specimen X 478. 9b. Oral view of juvenile specimen X 478. 9c. Lateral view of juvenile specimen X 478. 10a. Aboral view of juvenile specimen X 477. 10b. Oral view of juvenile specimen X 477. 10c. Lateral view of juvenile specimen X 477. 11a. Oral view of specimen transitional from *Spathognathodus* X 479. 11b. Aboral view of specimen transitional from *Spathognathodus* X 479. 11c. Lateral view of specimen transitional from *Spathognathodus* X 479. 12a. Aboral view of specimen X 480. 12b. Oral view of specimen X 480. 12c. Lateral view of specimen X 480. 13a. Aboral view of adult specimen X 481. 13b. Oral view of adult specimen X 481. 13c. Lateral view of adult specimen X 481.

FIGS. 14-16. *Pseudopolygnathus multistriatus* Mehl & Thomas

14a. Oral view of specimen X 486. 14b. Aboral view of specimen X 486. 14c. Lateral view of specimen X 486. 15a. Aboral view of specimen X 487. 15b. Oral view of specimen X 487. 15c. Lateral view of specimen X 487. 16a. Oral view of specimen X 485. 16b. Aboral view of specimen X 485. 16c. Lateral view of specimen X 485.

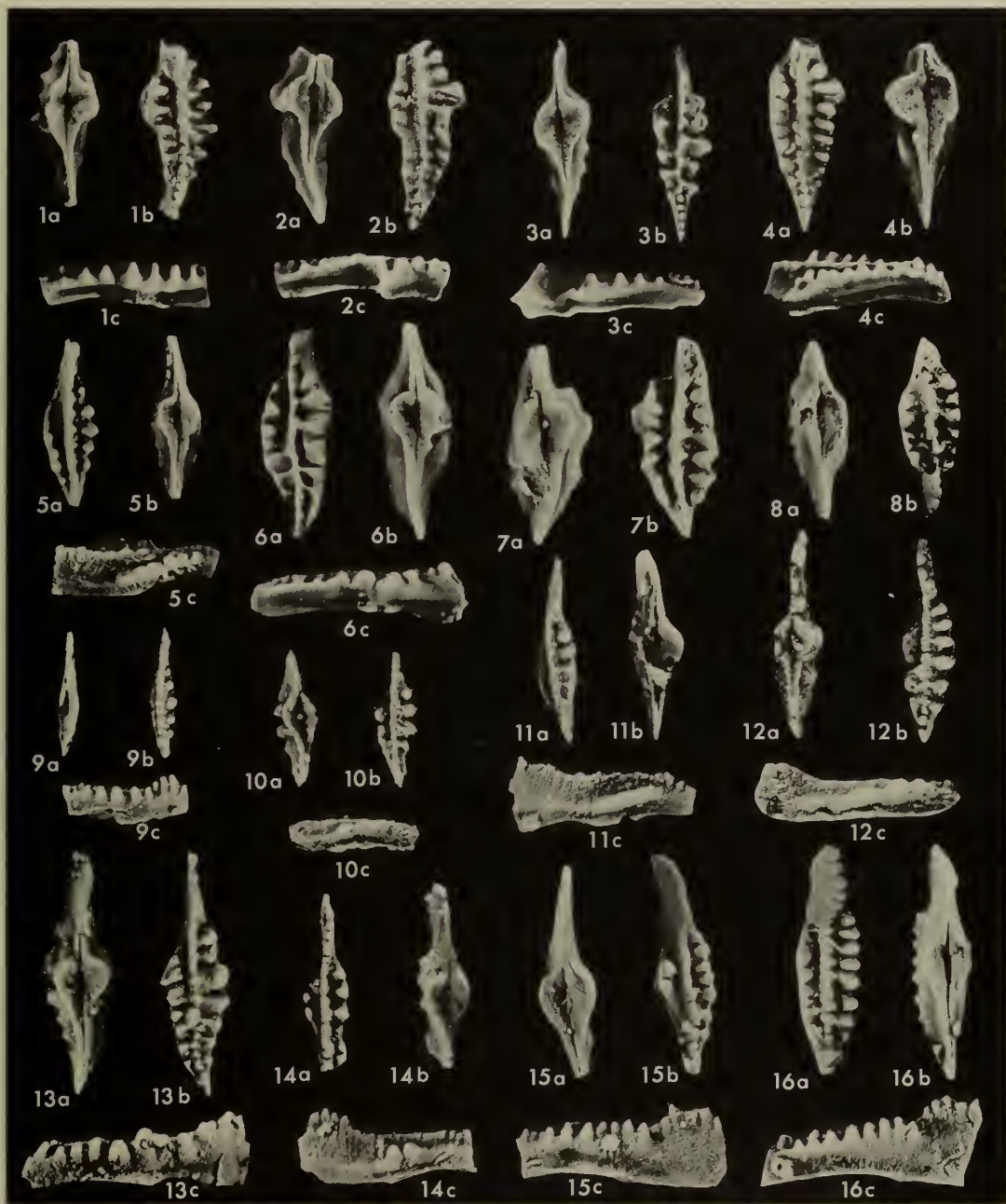


PLATE 6

All specimens coated and magnified $\times 31.5$

FIG. 1. *Pseudopolygnathus* cf. *fusiformis* Branson & Mehl

a. Aboral view of specimen X 552. b. Oral view of specimen X 552.

FIG. 2. *Pseudopolygnathus multistriatus* Mehl & Thomas

a. Oral view of specimen X 484. b. Aboral view of specimen X 484. c. Lateral view of specimen X 484.

FIG. 3. *Pseudopolygnathus* sp. A.

a. Oral view of specimen X 515. b. Aboral view of specimen X 515. c. Lateral view of specimen X 515.

FIGS. 4, 5, 7, 10-12. *Pseudopolygnathus primus* Branson & Mehl

4a. Aboral view of specimen X 546. 4b. Oral view of specimen X 546. 4c. Lateral view of specimen X 546. 5a. Aboral view of specimen X 497. 5b. Oral view of specimen X 497. 7a. Aboral view of specimen X 499. 7b. Oral view of specimen X 499. 7c. Lateral view of specimen X 499. 10a. Aboral view of specimen X 500. 10b. Oral view of specimen X 500. 10c. Lateral view of specimen X 500. 11a. Aboral view of specimen X 549. 11b. Oral view of specimen X 549. 11c. Lateral view of specimen X 549. 12a. Aboral view of specimen X 498. 12b. Oral view of specimen X 498. 12c. Lateral view of specimen X 498.

FIG. 6. *Pseudopolygnathus postinodosus* sp. nov.

a. Aboral view of holotype X 496. b. Oral view of holotype X 496. c. Lateral view of holotype X 496.

FIG. 8. *Pseudopolygnathus dentilineatus* E. R. Branson

a. Aboral view of specimen X 438. b. Oral view of specimen X 438. c. Lateral view of specimen X 438.

FIG. 9. *Spathognathodus* sp. nov.

a. Oral view of specimen X 518. b. Aboral view of specimen X 518. c. Lateral view of specimen X 518.

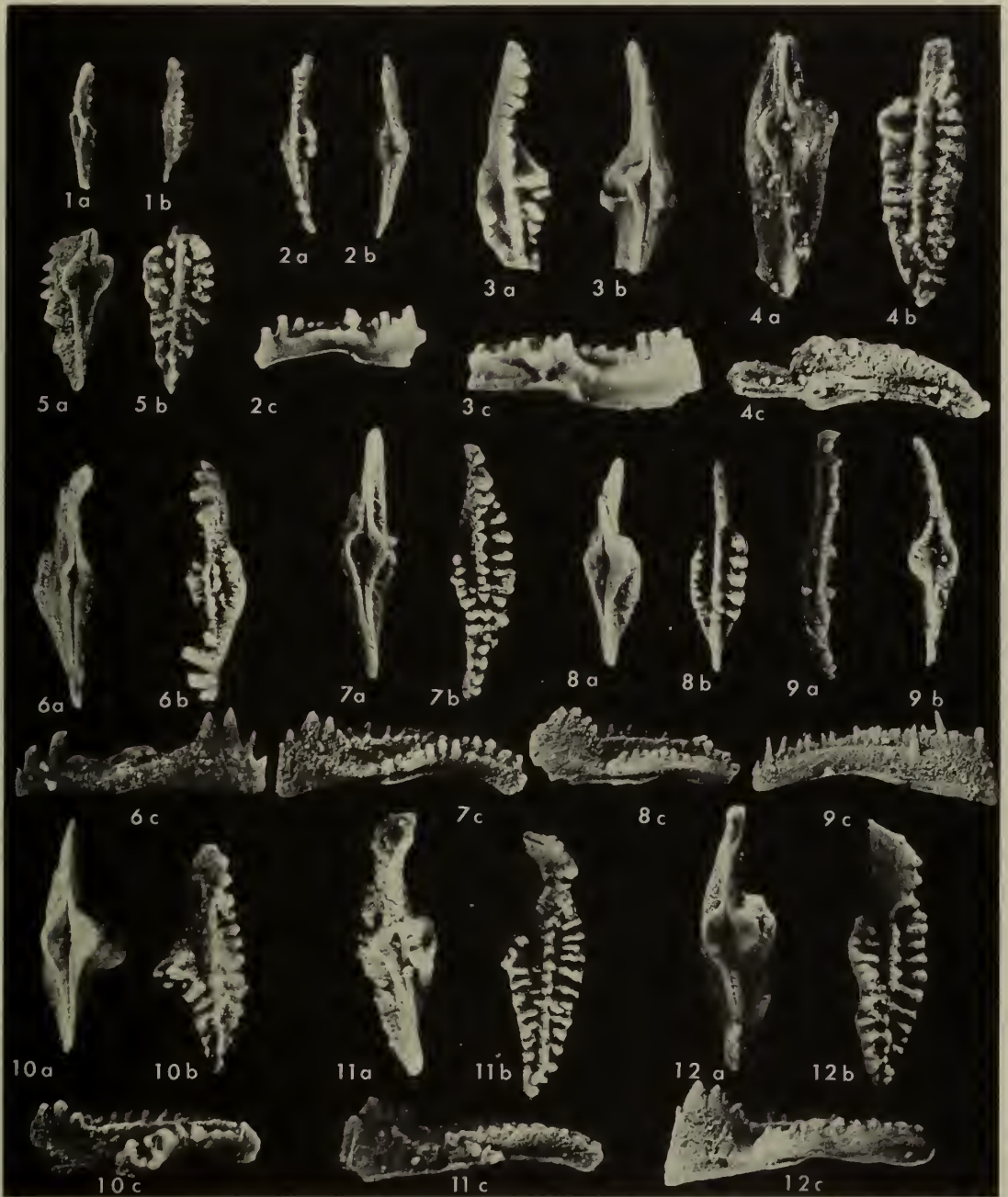


PLATE 7

All specimens coated and magnified $\times 31.5$

FIGS. 1-5. *Spathognathodus elongatus* (Branson & Mehl)

1a. Lateral view of specimen X 472. 1b. Oral view of specimen X 472. 2. Lateral view of specimen X 474. 3. Aboral view of specimen X 472. 4a. Lateral view of specimen X 473. 4b. Aboral view of specimen X 473. 5a. Lateral view of specimen X 475. 5b. Aboral view of specimen X 475.

FIGS. 6, 7. *Spathognathodus* cf. *robustus* (Branson & Mehl)

6a. Lateral view of specimen X 388. 6b. Oral view of specimen X 388. 6c. Aboral view of specimen X 388. 7a. Lateral view of specimen X 387. 7b. Oral view of specimen X 387. 7c. Aboral view of specimen X 387.

FIG. 8. *Spathognathodus* sp. B

a. Lateral view of specimen X 406. b. Oral view of specimen X 406. c. Aboral view of specimen X 406.

FIGS. 9-11. *Spathognathodus coaptus* (Branson & Mehl)

9a. Lateral view of specimen X 454. 9b. Aboral view of specimen X 454. 9c. Oral view of specimen X 454. 10a. Lateral view of specimen X 453. 10b. Aboral view of specimen X 453. 10c. Oral view of specimen X 453. 11a. Lateral view of specimen X 436. 11b. Aboral view of specimen X 436. 11c. Oral view of specimen X 436.

FIGS. 12-14. *Spathognathodus* cf. *cyrius* (Cooper)

12a. Lateral view of specimen X 471. 12b. Oral view of specimen X 471. 12c. Aboral view of specimen X 471. 13a. Lateral view of specimen X 470. 13b. Oral view of specimen X 470. 13c. Aboral view of specimen X 470. 14a. Lateral view of specimen X 469. 14b. Oral view of specimen X 469. 14c. Aboral view of specimen X 469.

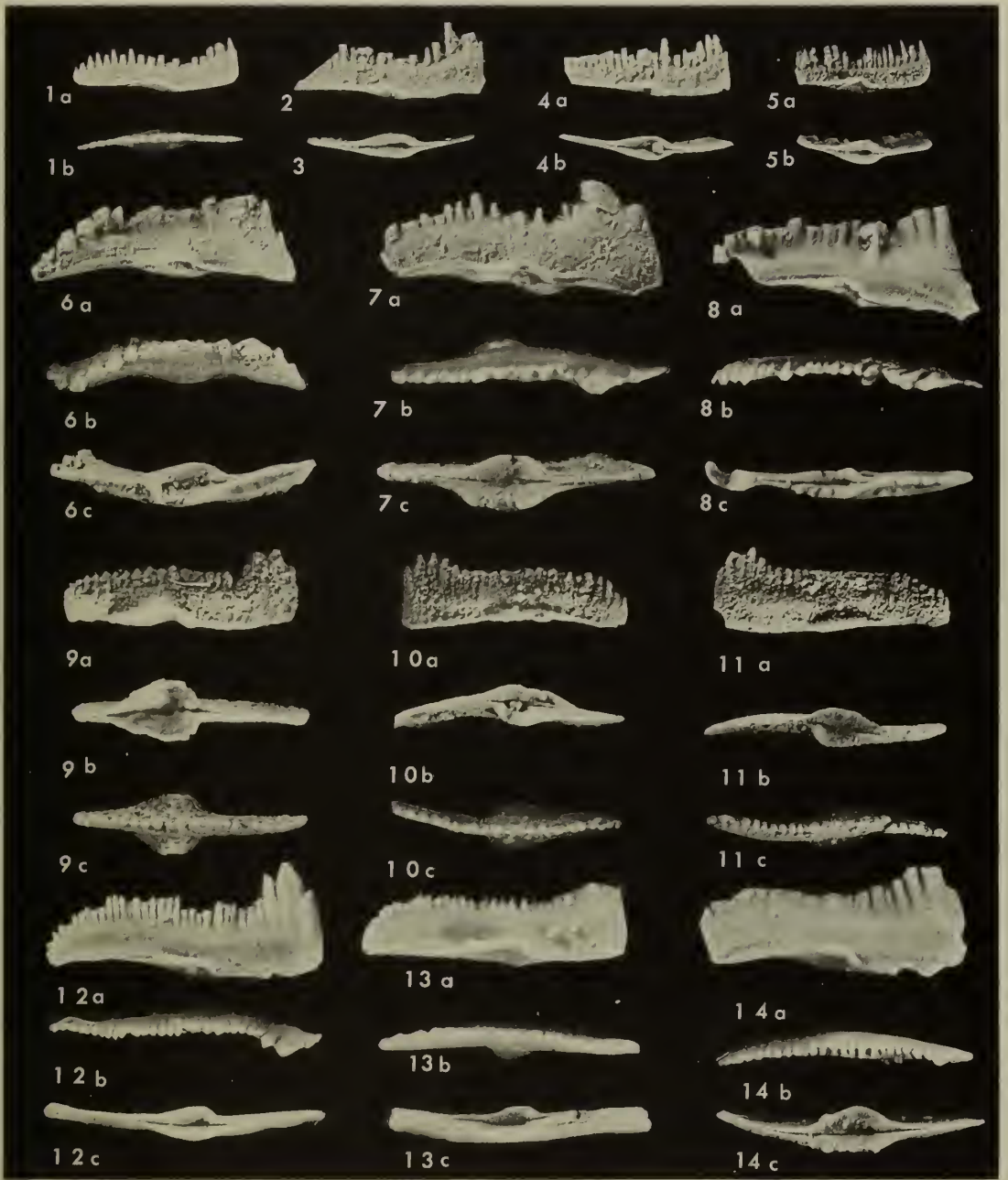


PLATE 8

All specimens coated and magnified $\times 31.5$

FIGS. 1-4. *Spathognathodus* cf. *campbelli* Rexroad

1a. Lateral view of specimen X 451. 1b. Aboral view of specimen X 451. 1c. Oral view of specimen X 451. 2a. Lateral view of specimen X 435. 2b. Aboral view of specimen X 435. 2c. Oral view of specimen X 435. 3a. Lateral view of specimen X 452. 3b. Oral view of specimen X 452. 3c. Aboral view of specimen X 452. 4a. Lateral view of specimen X 450. 4b. Oral view of specimen X 450. 4c. Aboral view of specimen X 450.

FIG. 5. *Gnathodus simplicatus* sp. nov.

a. Lateral view of paratype X 88. b. Oral view of paratype X 88. c. Aboral view of paratype X 88.

FIG. 6. *Gnathodus cuneiformis* Mehl and Thomas

a. Lateral view of specimen X 98. b. Oral view of specimen X 98. c. Aboral view of specimen X 98.

FIGS. 7, 8, 12, 13. *Spathognathodus* cf. *crustulus* Youngquist & Miller

7a. Lateral view of specimen X 554. 7b. Oral view of specimen X 554. 7c. Aboral view of specimen X 554. 8a. Lateral view of specimen X 555. 8b. Oral view of specimen X 555. 8c. Aboral view of specimen X 555. 12a. Lateral view of specimen X 556. 12b. Oral view of specimen X 556. 13a. Lateral view of specimen X 557. 13b. Oral view of specimen X 557.

FIGS. 9-11. *Spathognathodus scitulus* (Hinde)

9a. Lateral view of specimen X 391. 9b. Lateral view of specimen X 391. 9c. Oral view of specimen X 391. 9d. Aboral view of specimen X 391. 10a. Lateral view of specimen X 392. 10b. Lateral view of specimen X 392. 10c. Oral view of specimen X 392. 10d. Aboral view of specimen X 392. 11a. Lateral view of specimen X 393. 11b. Lateral view of specimen X 393. 11c. Oral view of specimen X 393. 11d. Aboral view of specimen X 393.

FIGS. 14-18. *Spathognathodus crustulus* Youngquist & Miller

14a. Lateral view of specimen X 466. 14b. Lateral view of specimen X 466. 15a. Lateral view of specimen X 467. 15b. Lateral view of specimen X 467. 15c. Oral view of specimen X 467. 15d. Aboral view of specimen X 467. 16a. Lateral view of specimen X 468. 16b. Lateral view of specimen X 468. 16c. Oral view of specimen X 468. 16d. Aboral view of specimen X 468. 17a. Lateral view of specimen X 464. 17b. Lateral view of specimen X 464. 17c. Oral view of specimen X 464. 17d. Aboral view of specimen X 464. 18a. Lateral view of specimen X 465. 18b. Lateral view of specimen X 465. 18c. Oral view of specimen X 465. 18d. Aboral view of specimen X 465.

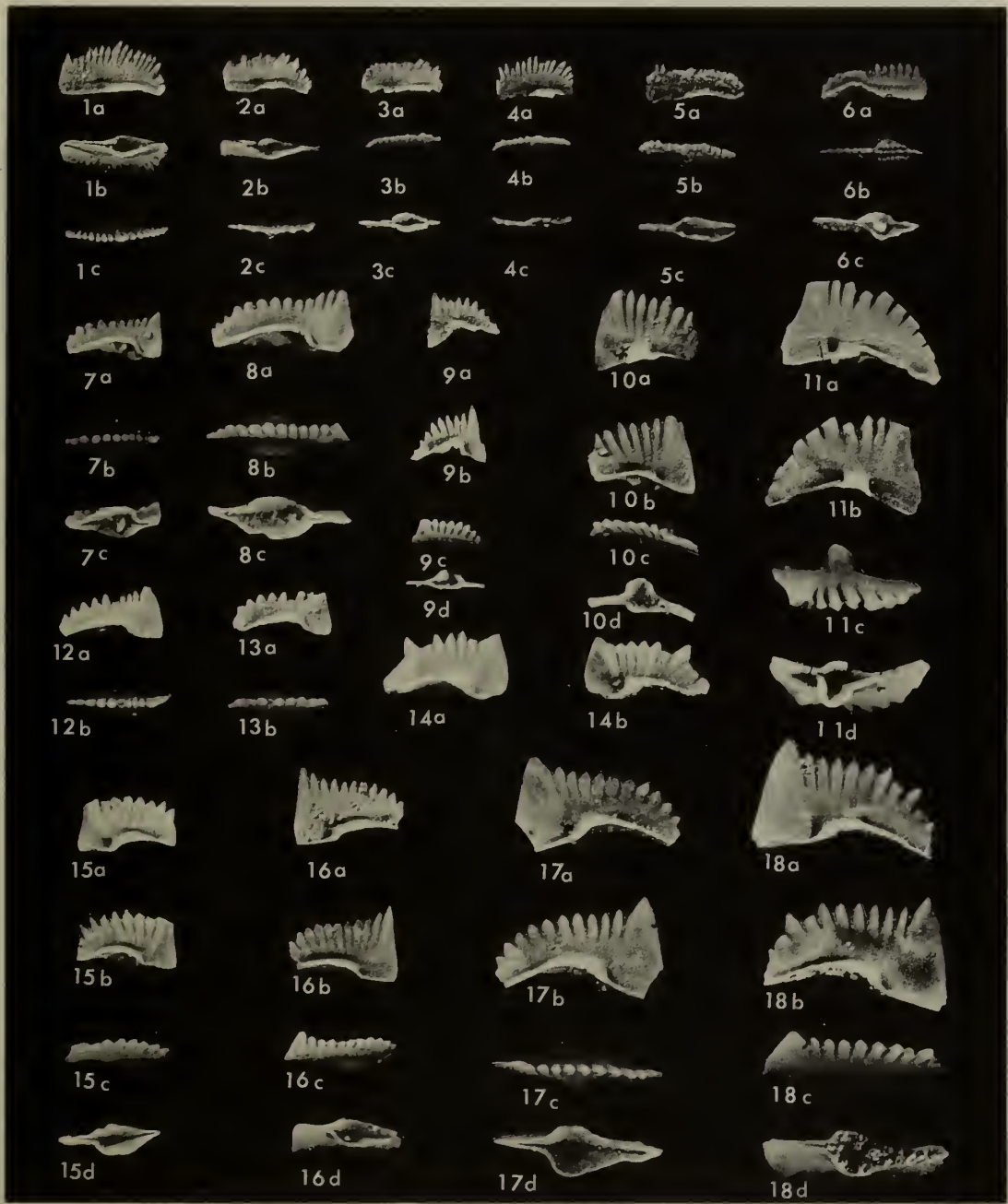


PLATE 9

All specimens coated and magnified $\times 31.5$

FIGS. 1-4. *Pseudopolygnathus nodomarginatus* (E. R. Branson)

1a. Oral view of specimen X 491. 1b. Aboral view of specimen X 491. 1c. Lateral view of specimen X 491. 2a. Oral view of specimen X 489. 2b. Aboral view of specimen X 489. 3c. Lateral view of specimen X 489. 3a. Oral view of specimen X 490. 3b. Aboral view of specimen X 490. 3c. Lateral view of specimen X 490. 4a. Oral view of specimen X 488. 4b. Aboral view of specimen X 488. 4c. Lateral view of specimen X 488.

FIGS. 5-8. *Polygnathus lobatus lobatus* Branson & Mehl

5a. Oral view of specimen X 378. 5b. Aboral view of specimen X 378. 5c. Lateral view of specimen X 378. 6a. Oral view of specimen X 376. 6b. Aboral view of specimen X 376. 6c. Lateral view of specimen X 376. 7a. Oral view of specimen X 377. 7b. Aboral view of specimen X 377. 7c. Lateral view of specimen X 377. 8a. Oral view of specimen X 440. 8b. Aboral view of specimen X 440. 8c. Lateral view of specimen X 440.

FIG. 9. *Polygnathus lobatus inflexus* subsp. nov.

a. Oral view of holotype X 375. b. Aboral view of holotype X 375. c. Lateral view of holotype X 375.

FIG. 10. *Cavusgnathus* ? sp. nov. A.

a. Oral view of specimen X 70. b. Aboral view of specimen X 70. c. Inner lateral view of specimen X 70. d. Outer lateral view of specimen X 70.

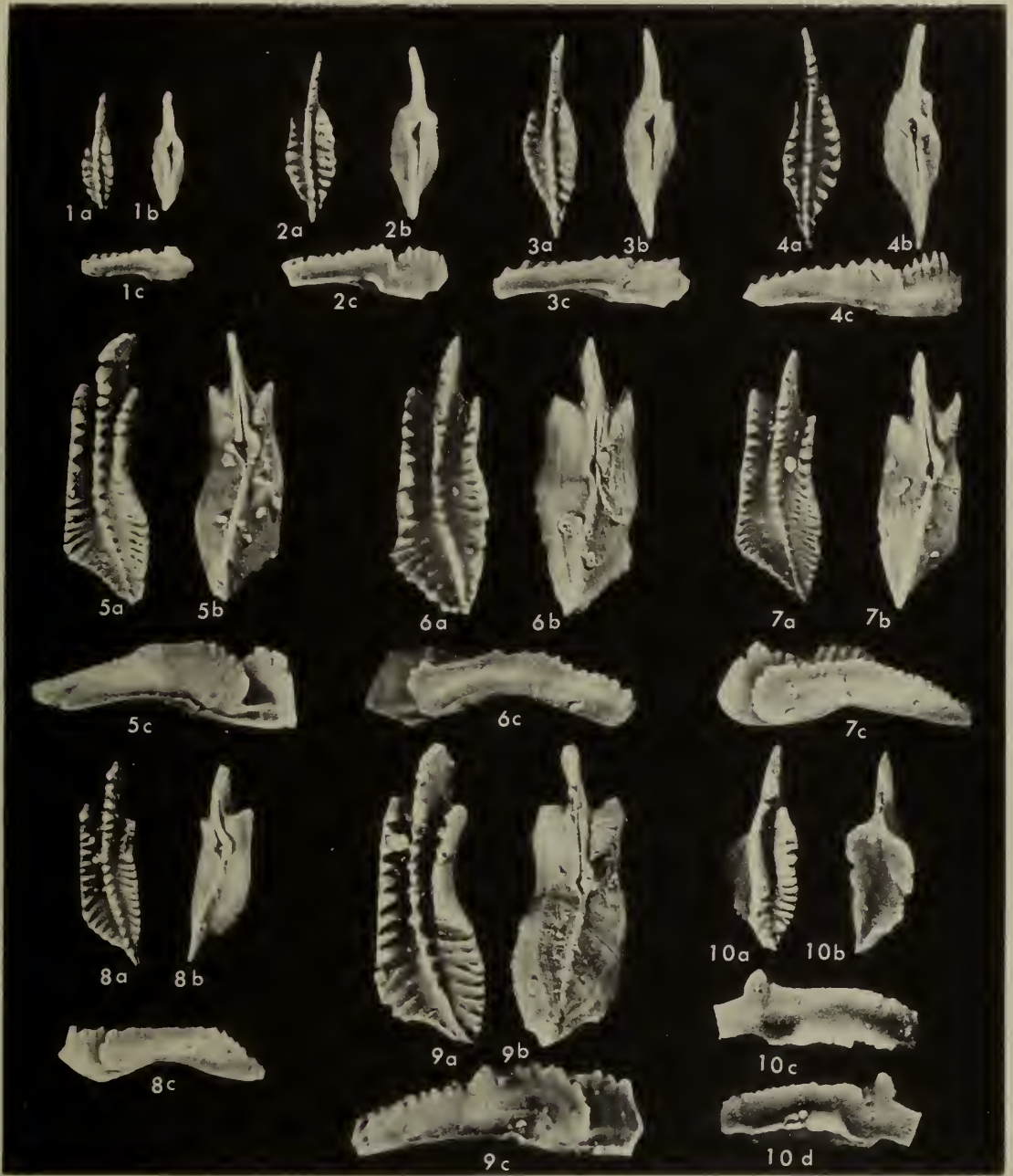


PLATE 10

All specimens coated and magnified $\times 31.5$

FIGS. 1-3. *Polygnathus inornatus vexatus* sub. sp. nov.

1a. Oral view of holotype X 358. 1b. Aboral view of holotype X 358. 1c. Lateral view of holotype X 358. 2a. Aboral view of paratype X 359. 2b. Oral view of paratype X 359. 2c. Lateral view of paratype X 359. 3a. Oral view of paratype X 551. 3b. Aboral view of paratype X 551. 3c. Lateral view of paratype X 551.

FIGS. 4-6. *Polygnathus inornatus inornatus* Branson & Mehl

4a. Aboral view of specimen X 353. 4b. Oral view of specimen X 353. 4c. Lateral view of specimen X 353. 5a. Aboral view of specimen X 355. 5b. Oral view of specimen X 355. 5c. Lateral view of specimen X 355. 6a. Oral view of specimen X 354. 6b. Aboral view of specimen X 354. 6c. Lateral view of specimen X 354.

FIGS. 7-9. *Polygnathus inornatus rostratus* subsp. nov.

7a. Aboral view of holotype X 530. 7b. Oral view of holotype X 530. 7c. Lateral view of holotype X 530. 8a. Aboral view of paratype X 357. 8b. Oral view of paratype X 357. 9a. Aboral view of paratype X 356. 9b. Oral view of paratype X 356. 9c. Lateral view of paratype X 356.

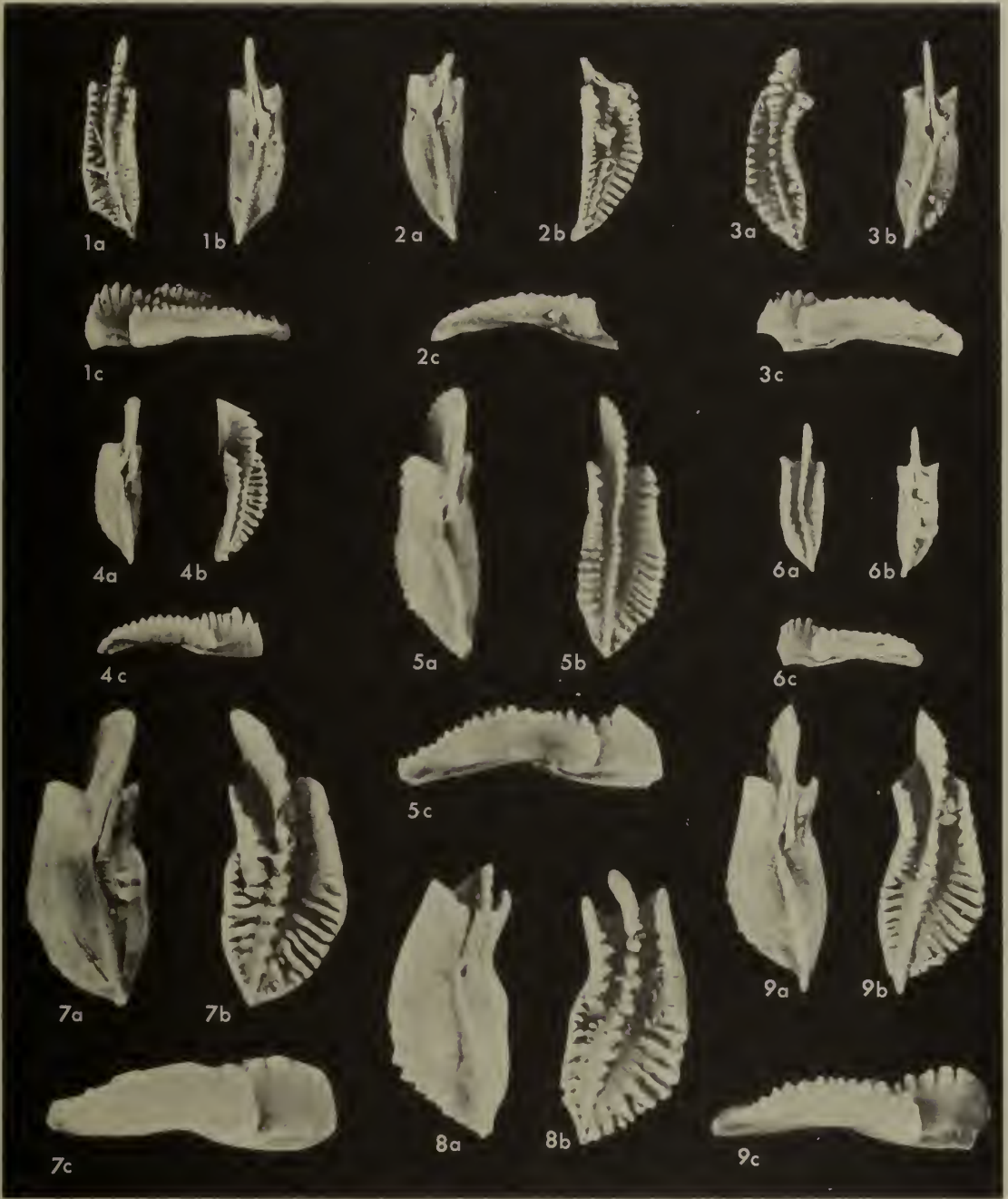


PLATE 11

All specimens coated and magnified $\times 31.5$

FIGS. 1-4. *Polygnathus lacinatus asymmetricus* subsp. nov.

1a. Aboral view of paratype X 360. 1b. Oral view of paratype X 360. 1c. Lateral view of paratype X 360. 2a. Aboral view of paratype X 363. 2b. Oral view of paratype X 363. 2c. Lateral view of paratype X 363. 3a. Aboral view of holotype X 361. 3b. Oral view of holotype X 361. 3c. Lateral view of holotype X 361. 4a. Aboral view of paratype X 362. 4b. Oral view of paratype X 362. 4c. Lateral view of paratype X 362.

FIGS. 5-7, 11. *Polygnathus lacinatus prelobatus* subsp. nov.

5a. Oral view of paratype X 372. 5b. Aboral view of paratype X 372. 6a. Oral view of paratype X 374. 6b. Aboral view of paratype X 374. 7a. Oral view of paratype X 373. 7b. Lateral view of paratype X 373. 11a. Oral view of holotype X 371. 11b. Aboral view of holotype X 371. 11c. Lateral view of holotype X 371.

FIGS. 8-10. *Polygnathus lacinatus lacinatus* Huddle

8a. Oral view of specimen X 370. 8b. Lateral view of specimen X 370. 9a. Oral view of specimen X 369. 9b. Aboral view of specimen X 369. 9c. Lateral view of specimen X 369. 10a. Aboral view of specimen X 368. 10b. Oral view of specimen X 368. 10c. Lateral view of specimen X 368.

FIGS. 12-15. *Polygnathus lacinatus circaperipherus* subsp. nov.

12a. Aboral view of paratype X 367. 12b. Oral view of paratype X 367. 12c. Lateral view of paratype X 367. 13a. Aboral view of paratype X 365. 13b. Oral view of paratype X 365. 13c. Lateral view of paratype X 365. 14a. Aboral view of holotype X 364. 14b. Oral view of holotype X 364. 14c. Lateral view of holotype X 364. 15a. Oral view of paratype X 366. 15b. Aboral view of paratype X 366. 15c. Lateral view of paratype X 366.

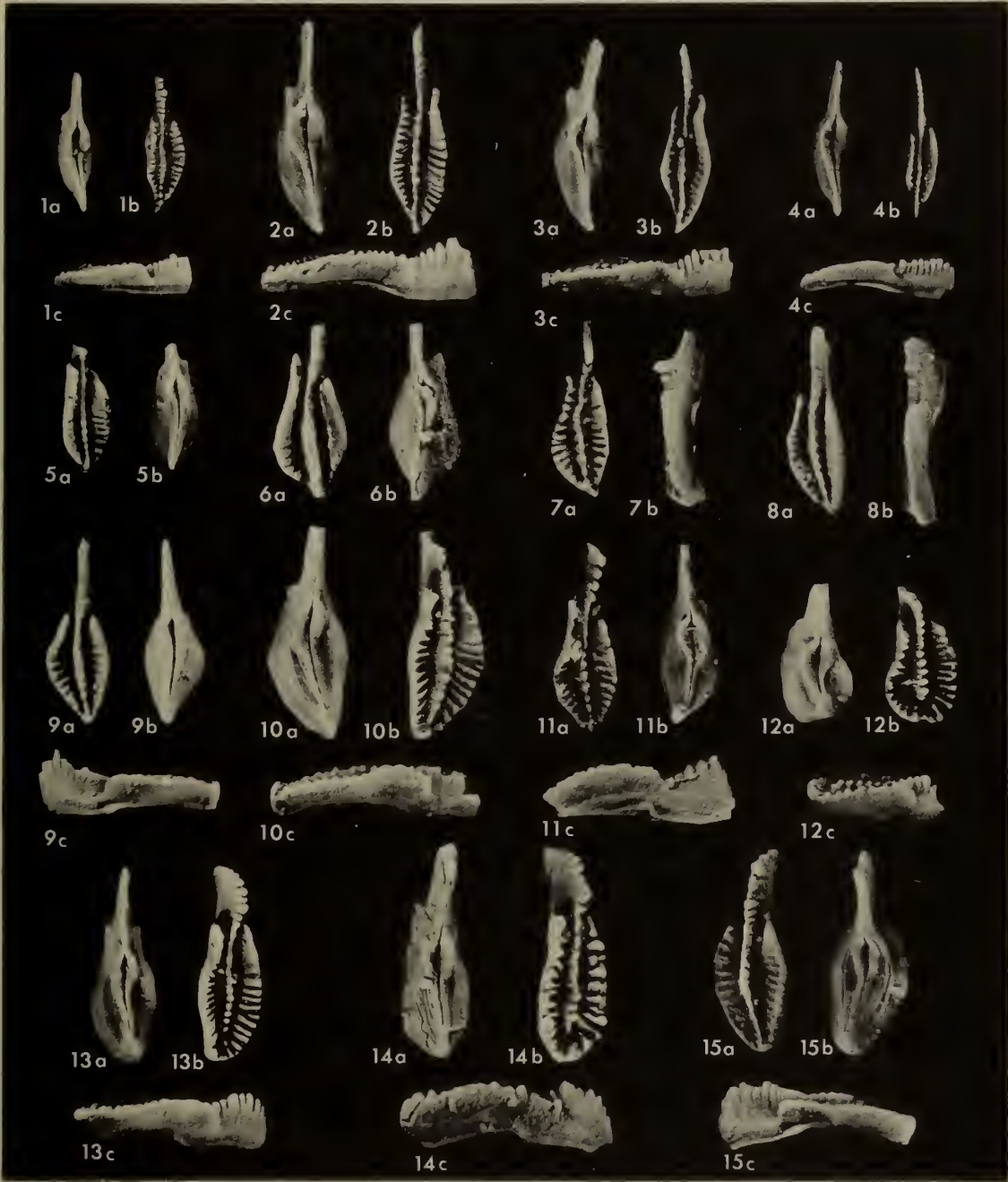


PLATE 12

All specimens coated and magnified $\times 31.5$

FIG. 1. *Polygnathus* cf. *communis* Branson & Mehl

a. Aboral view of specimen X 516. b. Oral view of specimen X 516. c. Lateral view of specimen X 516.

FIGS. 2-5. *Polygnathus communis communis* Branson & Mehl

2a. Oral view of specimen X 348. 2b. Aboral view of specimen X 348. 2c. Lateral view of specimen X 348. 3a. Oral view of specimen X 347. 3b. Aboral view of specimen X 347. 3c. Lateral view of specimen X 347. 4a. Aboral view of specimen X 430. 4b. Oral view of specimen X 430. 4c. Lateral view of specimen X 430. 5a. Oral view of specimen X 346. 5b. Aboral view of specimen X 346. 5c. Lateral view of specimen X 346.

FIGS. 6-8, 10. *Pseudopolygnathus nodomarginatus* (E. R. Branson)

6a. Oral view of specimen X 495. 6b. Aboral view of specimen X 495. 6c. Lateral view of specimen X 495. 7a. Aboral view of specimen X 493. 7b. Oral view of specimen X 493. 7c. Lateral view of specimen X 493. 8a. Oral view of specimen X 494 showing rounding of posterior termination. 8b. Aboral view of specimen X 494 showing rounding of posterior termination. 8c. Lateral view of specimen X 494. 10a. Aboral view of specimen X 492. 10b. Oral view of specimen X 492. 10c. Lateral view of specimen X 492.

FIGS. 9, 11. *Siphonodella isosticha* (Cooper)

9a. Oral view of specimen X 534. 9b. Aboral view of specimen X 534. 11a. Oral view of specimen X 535. 11b. Aboral view of specimen X 535.

FIG. 12. *Siphonodella* sp. A

a. Aboral view of specimen X 537. b. Oral view of specimen X 537.

FIG. 13. *Siphonodella obsoleta* Hass

a. Aboral view of specimen X 536. b. Oral view of specimen X 536. c. Lateral view of specimen X 536.

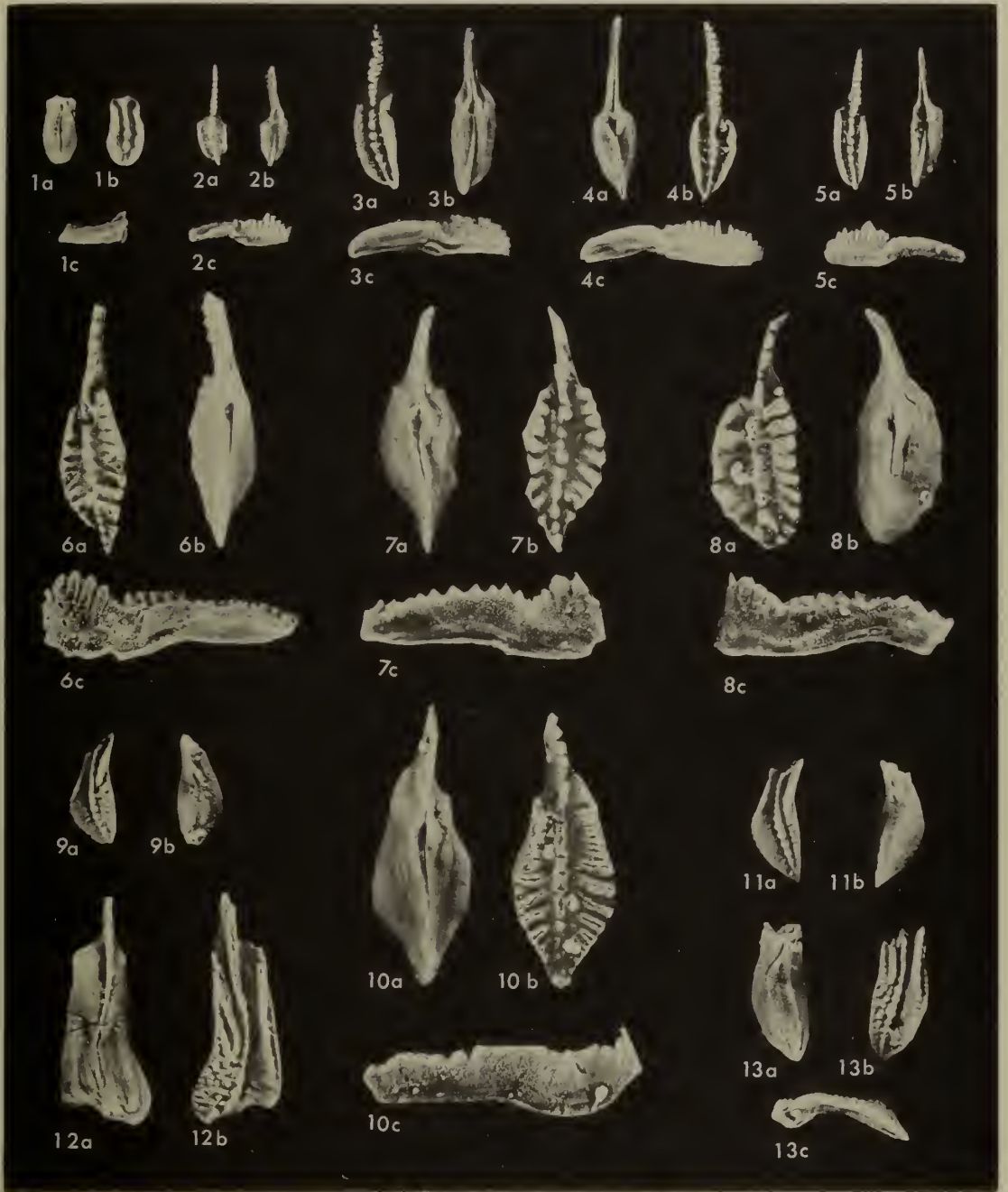


PLATE 13

All specimens coated and magnified $\times 31.5$

FIGS. 1-3. *Taphrognathus* - *Cavusgnathus* transitions

1. Oral view of specimen X 558. 2. Oral view of specimen X 559. 3a. Oral view of specimen X 560. 3b. Aboral view of specimen X 560. 3c. Outer lateral view of specimen X 560.

FIGS. 4, 5. *Taphrognathus varians* Branson & Mehl

4a. Oral view of specimen X 407. 4b. Aboral view of specimen X 407. 4c. Outer lateral view of specimen X 407. 4d. Inner lateral view of specimen X 407. 5a. Oral view of specimen X 408. 5b. Aboral view of specimen X 408. 5c. Outer lateral view of specimen X 408. 5d. Inner lateral view of specimen X 408.

FIGS. 6, 7, 13. *Cavusgnathus charactus* Rexroad

6a. Oral view of specimen X 59. 6b. Aboral view of specimen X 59. 6c. Outer lateral view of specimen X 59. 6d. Inner lateral view of specimen X 59. 7a. Oral view of specimen X 61. 7b. Aboral view of specimen X 61. 7c. Outer lateral view of specimen X 61. 7d. Inner lateral view of specimen X 61. 13a. Oral view of specimen X 62. 13b. Aboral view of specimen X 62. 13c. Inner lateral view of specimen X 62.

FIGS. 8-11. *Polygnathus bischoffi* sp. nov.

8a. Oral view of hypotype X 352. 8b. Aboral view of hypotype X 352. 8c. Lateral view of hypotype X 352. 9a. Oral view of paratype X 351. 9b. Aboral view of paratype X 351. 9c. Lateral view of paratype X 351. 10a. Oral view of paratype X 350. 10b. Aboral view of paratype X 350. 10c. Lateral view of paratype X 350. 11a. Oral view of holotype X 349. 11b. Aboral view of holotype X 349. 11c. Lateral view of holotype X 349.

FIG. 12. *Cavusgnathus naviculus* (Hinde)

a. Oral view of specimen X 65. b. Outer lateral view of specimen X 65. c. Aboral view of specimen X 65. d. Inner lateral view of specimen X 65.

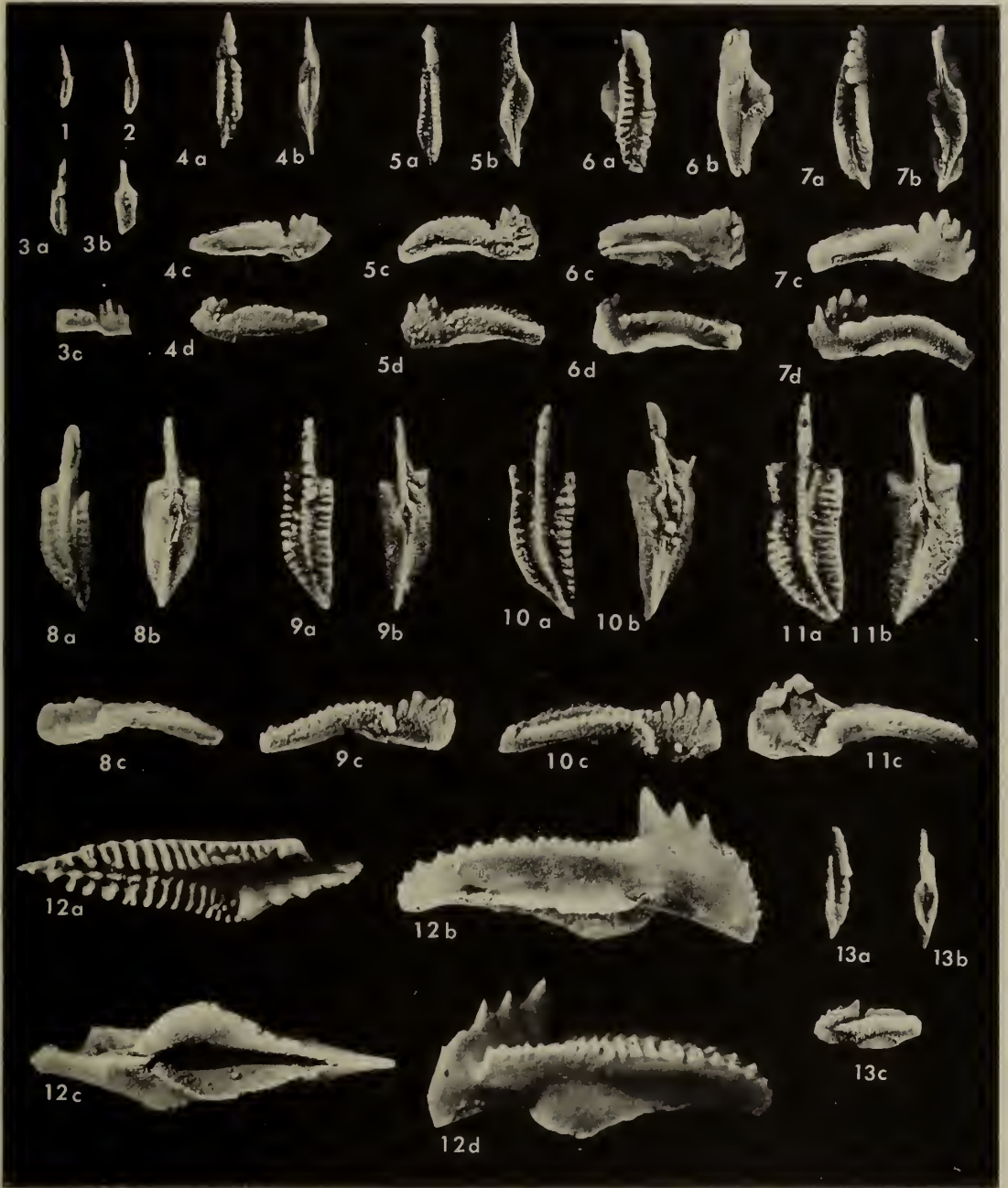


PLATE 14

All specimens coated and magnified $\times 31.5$

FIGS. 1, 4-6. *Cavusgnathus naviculus* (Hinde)

1a. Oral view of specimen X 66. 1b. Aboral view of specimen X 66. 1c. Inner lateral view of specimen X 66. 1d. Outer lateral view of specimen X 66. 4a. Oral view of specimen X 69. 4b. Aboral view of specimen X 69. 4c. Inner lateral view of specimen X 69. 4d. Outer lateral view of specimen X 69. 5a. Oral view of specimen X 68. 5b. Aboral view of specimen X 68. 5c. Inner lateral view of specimen X 68. 5d. Outer lateral view of specimen X 68. 6a. Oral view of specimen X 67. 6b. Aboral view of specimen X 67. 6c. Inner lateral view of specimen X 67. 6d. Outer lateral view of specimen X 67.

FIG. 2. *Cavusgnathus convexus* Rexroad

a. Oral view of specimen X 63. b. Aboral view of specimen X 63. c. Inner lateral view of specimen X 63. d. Outer lateral views of specimen X 63.

FIG. 3. *Cavusgnathus cristatus* Branson and Mehl

a. Oral view of specimen X 64. b. Aboral view of specimen X 64. c. Inner lateral view of specimen X 64. d. Outer lateral view of specimen X 64.

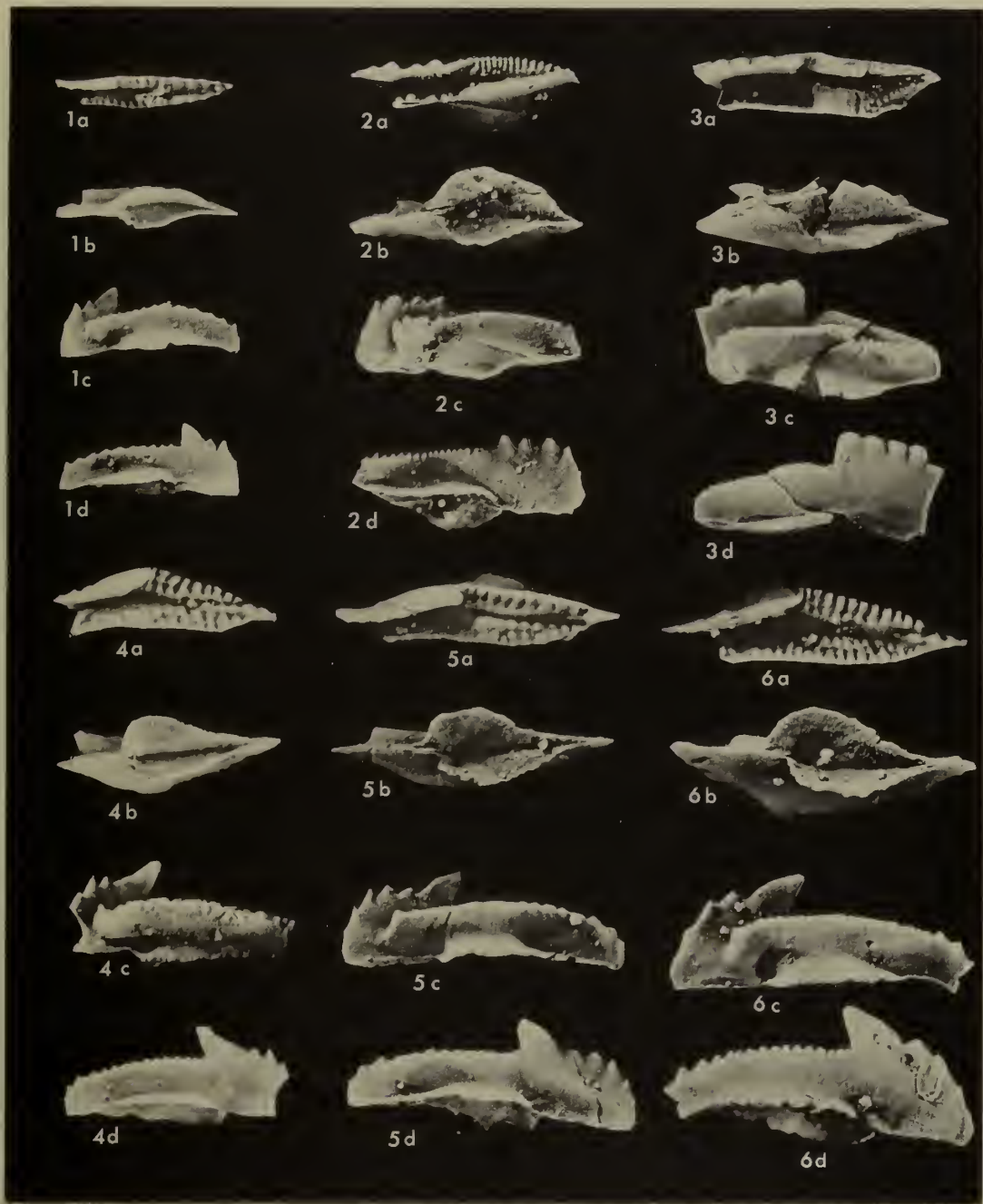


PLATE 15

All specimens coated and magnified $\times 31.5$

FIGS. 1-3, 8. *Mestognathus bipluti* Higgins

1a. Outer aboral lateral view of specimen X 246. 1b. Outer lateral oral view of specimen X 246. 1c. Inner lateral oral view of specimen X 246. 2a. Aboral view of specimen X 248. 2b. Outer lateral view of specimen X 248. 2c. Inner lateral view of specimen X 248. 3a. Outer aboral lateral view of specimen X 247. 3b. Outer lateral oral view of specimen X 247. 3c. Inner lateral oral view of specimen X 247. 8a. Aboral view of specimen X 249. 8b. Inner oral view of specimen X 249.

FIGS. 4-6. *Mestognathus neddensis* sp. nov.

4a. Aboral view of paratype X 251. 4b. Inner lateral oral view of paratype X 251. 4c. Outer lateral view of paratype X 251. 5a. Outer aboral lateral view of paratype X 252. 5b. Inner lateral oral view of paratype X 252. 5c. Outer lateral oral view of paratype X 252. 6a. Aboral view of holotype X 250. 6b. Inner lateral oral view of holotype X 250. 6c. Outer lateral view of holotype X 250.

FIG. 7. *Mestognathus beckmanni* Bischoff

a. Aboral view of specimen X 245. b. Oral view of specimen X 245. c. Outer lateral view of specimen X 245. d. Inner lateral view of specimen X 245.

FIG. 9. *Polygnathus* sp.

a. Oral view of specimen X 531. b. Inner lateral view of specimen X 531. c. Aboral view of specimen X 531.

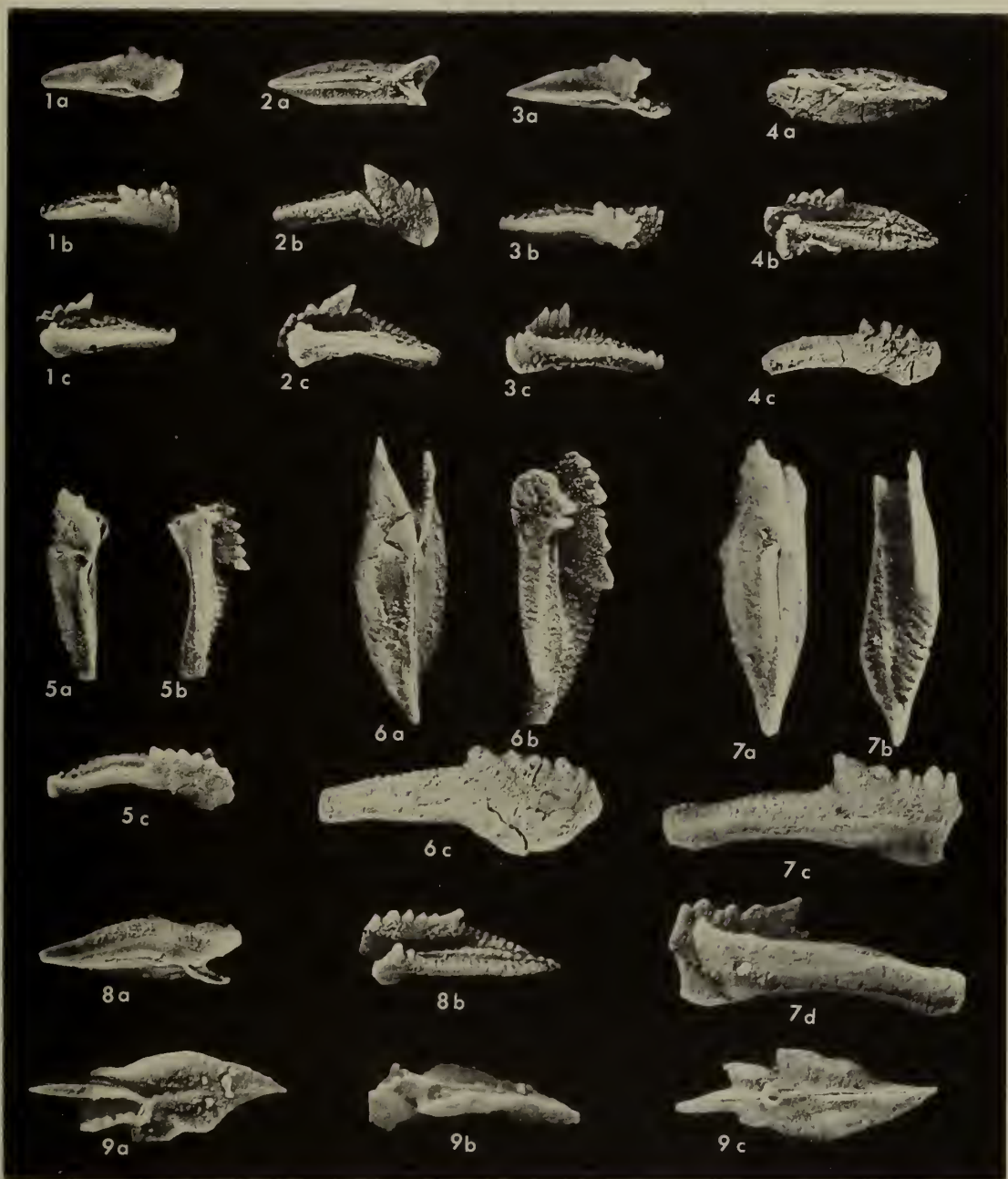


PLATE 16

All specimens coated and magnified $\times 31.5$

FIGS. 1-4. *Gnathodus girtyi simplex* Dunn

1a. Aboral view of specimen X 108. 1b. Oral view of specimen X 108. 1c. Outer lateral view of specimen X 108. 1d. Inner lateral view of specimen X 108. 2a. Oral view of specimen X 107. 2b. Aboral view of specimen X 107. 2c. Inner lateral view of specimen X 107. 2d. Outer lateral view of specimen X 107. 3a. Oral view of specimen X 110. 3b. Aboral view of specimen X 110. 3c. Inner lateral view of specimen X 110. 3d. Outer lateral view of specimen X 110. 4a. Oral view of specimen X 111. 4b. Aboral view of specimen X 111. 4c. Inner lateral view of specimen X 111. 4d. Outer lateral view of specimen X 111.

FIGS. 5-8. *Gnathodus girtyi collinsoni* subsp. nov.

5a. Oral view of paratype X 102. 5b. Aboral view of paratype X 102. 5c. Inner lateral view of paratype X 102. 5d. Outer lateral view of paratype X 102. 6a. Aboral view of holotype X 99. 6b. Oral view of holotype X 99. 6c. Outer lateral view of holotype X 99. 6d. Inner lateral view of holotype X 99. 7a. Aboral view of paratype X 101. 7b. Oral view of paratype X 101. 7c. Outer lateral view of paratype X 101. 7d. Inner lateral view of paratype X 101. 8a. Aboral view of paratype X 100. 8b. Oral view of paratype X 100. 8c. Outer lateral view of paratype X 100. 8d. Inner lateral view of paratype X 100.

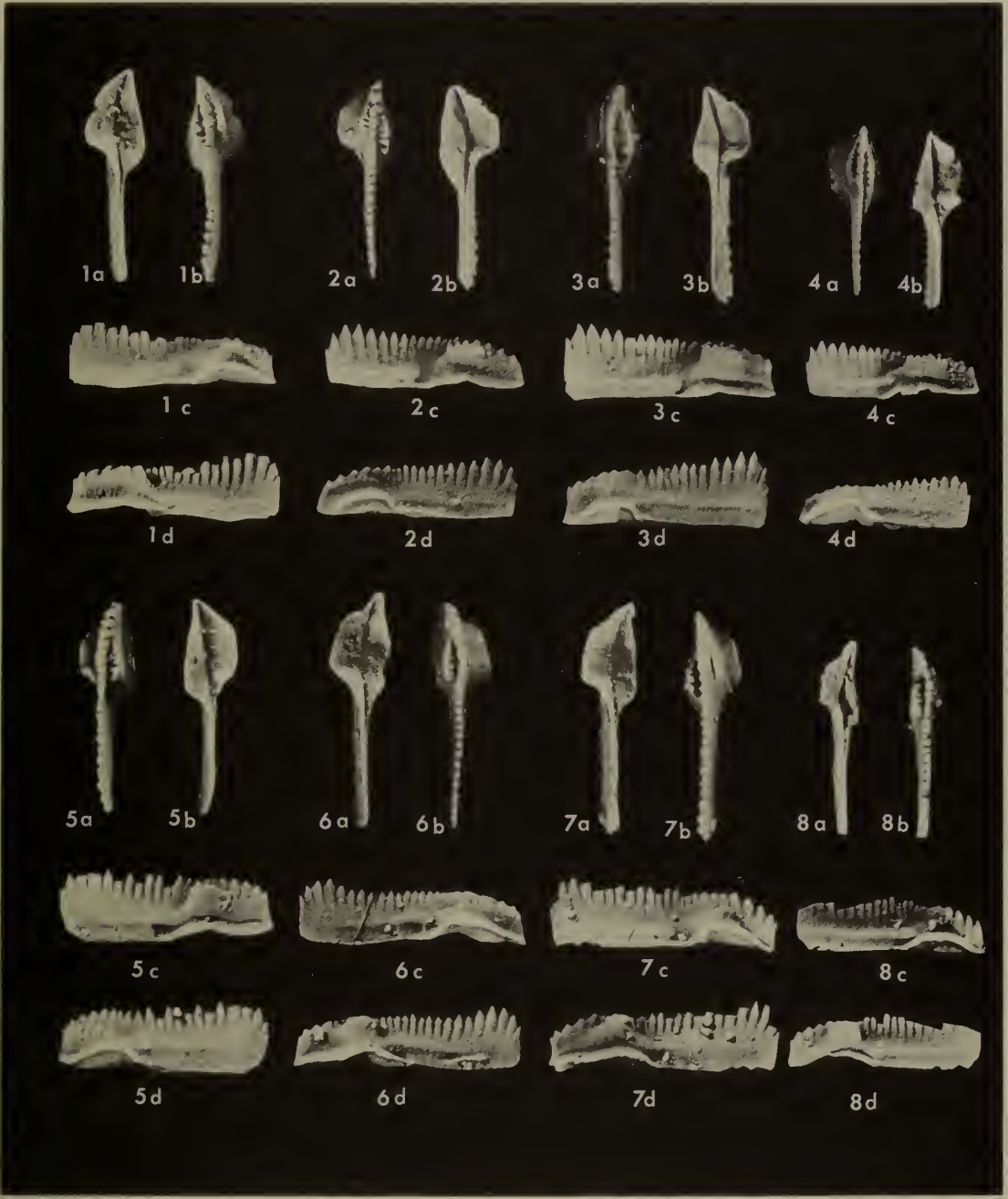


PLATE 17

All specimens coated and magnified $\times 31.5$

FIGS. 1-3. *Gnathodus girtyi* subsp. nov. A

1a. Aboral view of specimen X 118. 1b. Oral view of specimen X 118. 1c. Inner lateral view of specimen X 118. 2a. Aboral view of specimen X 119. 2b. Oral view of specimen X 119. 2c. Outer lateral view of specimen X 119. 2d. Inner lateral view of specimen X 119. 3a. Aboral view of specimen X 117. 3b. Oral view of specimen X 117. 3c. Outer lateral view of specimen X 117. 3d. Inner lateral view of specimen X 117.

FIG. 4. *Gnathodus* sp.

a. Aboral view of specimen X 138. b. Oral view of specimen X 138. c. Inner lateral view of specimen X 138. d. Outer lateral view of specimen X 138.

FIGS. 5-8. *Gnathodus girtyi soniae* subsp. nov.

5a. Aboral view of paratype X 115. 5b. Oral view of paratype X 115. 5c. Outer lateral view of paratype X 115. 5d. Inner lateral view of paratype X 115. 6a. Aboral view of holotype X 113. 6b. Oral view of holotype X 113. 6c. Outer lateral view of holotype X 113. 7a. Aboral view of paratype X 112. 7b. Oral view of paratype X 112. 7c. Outer lateral view of paratype X 112. 7d. Inner lateral view of paratype X 112. 8a. Oral view of paratype X 114. 8b. Aboral view of paratype X 114. 8c. Inner lateral view of paratype X 114. 8d. Outer lateral view of paratype X 114.

FIGS. 9-12. *Gnathodus girtyi girtyi* Hass

9a. Aboral view of specimen X 106. 9b. Oral view of specimen X 106. 9c. Outer lateral view of specimen X 106. 9d. Inner lateral views of specimen X 106. 10a. Aboral view of specimen X 105. 10b. Oral view of specimen X 105. 10c. Outer lateral view of specimen X 105. 10d. Inner lateral view of specimen X 105. 11a. Aboral view of specimen X 104. 11b. Oral view of specimen X 104. 11c. Outer lateral view of specimen X 104. 11d. Inner lateral view of specimen X 104. 12a. Aboral view of specimen X 103. 12b. Oral view of specimen X 103. 12c. Outer lateral view of specimen X 103. 12d. Inner lateral view of specimen X 103.

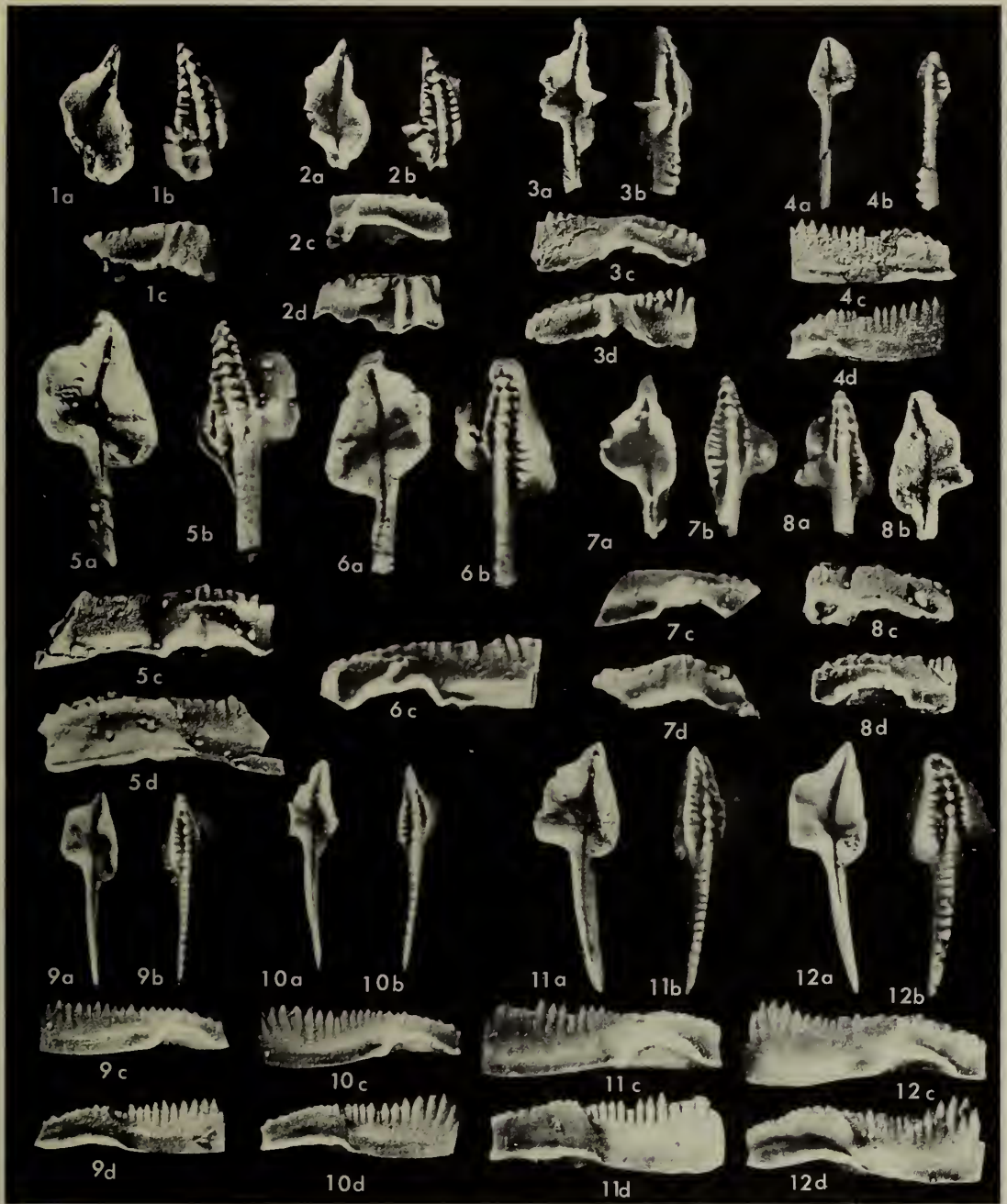


PLATE 18

All specimens coated and magnified $\times 31.5$

FIGS. 1, 10, 11. *Gnathodus punctatus* (Cooper)

1a. Aboral view of specimen X 132. 1b. Oral view of specimen X 132. 1c. Outer lateral view of specimen X 132. 10a. Aboral view of specimen X 131. 10b. Oral view of specimen X 131. 10c. Inner lateral view of specimen X 131. 10d. Outer lateral view of specimen X 131. 11a. Aboral view of specimen X 133. 11b. Oral view of specimen X 133. 11c. Inner lateral view of specimen X 133. 11d. Outer lateral view of specimen X 133.

FIGS. 2-5. *Gnathodus simplicatus* sp. nov.

2a. Aboral view of holotype X 89. 2b. Oral view of holotype X 89. 2c. Lateral view of holotype X 89. 3a. Lateral view of paratype X 91. 3b. Oral view of paratype X 91. 4a. Lateral view of paratype X 90. 4b. Oral view of paratype X 90. 5a. Lateral view of paratype X 415. 5b. Oral view of paratype X 415.

FIGS. 6, 8, 13. *Gnathodus antetexanus* Rexroad & Scott

6a. Aboral view of specimen X 412. 6b. Oral view of specimen X 412. 6c. Outer lateral view of specimen X 412. 8a. Outer lateral view of specimen X 413. 8b. Oral view of specimen X 413. 13a. Aboral view of specimen X 414. 13b. Oral view of specimen X 414. 13c. Outer lateral view of specimen X 414. 13d. Inner lateral view of specimen X 414.

FIG. 7. *Gnathodus* ? sp. nov.

a. Aboral view of specimen X 92. b. Oral view of specimen X 92. c. Outer lateral view of specimen X 92.

FIG. 9. *Gnathodus avonensis* sp. nov.

a. Aboral view of holotype X 411. b. Oral view of holotype X 411. c. Lateral view of holotype X 411. d. Lateral view of holotype X 411.

FIG. 12. *Gnathodus delicatus* Branson & Mehl

a. Aboral view of specimen X 87. b. Oral view of specimen X 87. c. Inner lateral view of specimen X 87. d. Outer lateral view of specimen X 87.

FIGS. 14-17. *Gnathodus bilineatus* (Roundy)

14a. Aboral view of specimen X 94. 14b. Oral view of specimen X 94. 14c. Outer lateral view of specimen X 94. 14d. Inner lateral view of specimen X 94. 15a. Aboral view of specimen X 93. 15b. Oral view of specimen X 93. 15c. Inner lateral view of specimen X 93. 15d. Outer lateral view of specimen X 93. 16a. Aboral view of specimen X 417. 16b. Oral view of specimen X 417. 16c. Inner lateral view of specimen X 417. 16d. Outer lateral view of specimen X 417. 17a. Aboral view of specimen X 416. 17b. Oral view of specimen X 416. 17c. Inner lateral view of specimen X 416. 17d. Outer lateral view of specimen X 416.

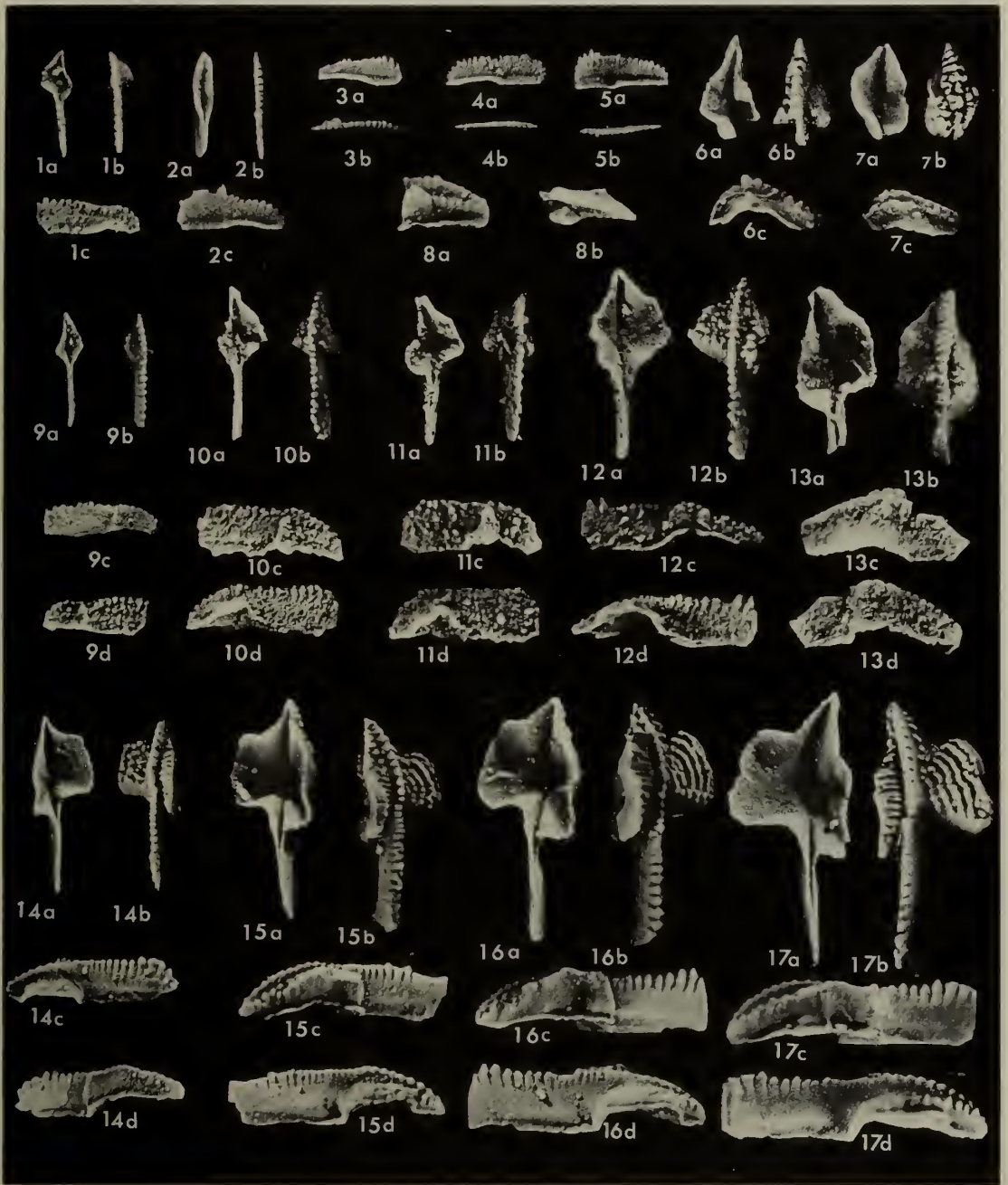


PLATE 19

All specimens coated and magnified $\times 31.5$

FIGS. 1-4. *Gnathodus symmutatus* sp. nov.

1a. Lateral view of paratype X 135. 1b. Aboral view of paratype X 135. 2a. Oral view of paratype X 136. 2b. Lateral view of paratype X 136. 2c. Aboral view of paratype X 136. 3a. Lateral view of paratype X 137. 3b. Aboral view of paratype X 137. 4a. Lateral view of holotype X 134. 4b. Aboral view of holotype X 134. 4c. Oral view of holotype X 134.

FIGS. 5-8. *Gnathodus homopunctatus* Ziegler

5a. Lateral view of specimen X 121. 5b. Lateral view of specimen X 121. 5c. Oral view of specimen X 121. 6a. Lateral view of specimen X 122. 6b. Lateral view of specimen X 122. 6c. Oral view of specimen X 122. 6d. Aboral view of specimen X 122. 7a. Lateral view of specimen X 123. 7b. Lateral view of specimen X 123. 7c. Aboral view of specimen X 123. 7d. Oral view of specimen X 123. 8a. Lateral view of specimen X 120. 8b. Lateral view of specimen X 120. 8c. Aboral view of specimen X 120. 8d. Oral view of specimen X 120.

FIGS. 9-12. *Gnathodus commutatus* (Branson & Mehl)

9a. Lateral view of specimen X 96. 9b. Lateral view of specimen X 96. 9c. Aboral view of specimen X 96. 9d. Oral view of specimen X 96. 10a. Lateral view of specimen X 418. 10b. Lateral view of specimen X 418. 10c. Aboral view of specimen X 418. 10d. Oral view of specimen X 418. 11a. Lateral view of specimen X 95. 11b. Lateral view of specimen X 95. 11c. Aboral view of specimen X 95. 11d. Oral view of specimen X 95. 12a. Lateral view of specimen X 97. 12b. Lateral view of specimen X 97. 12c. Oral view of specimen X 97. 12d. Aboral view of specimen X 97.

FIGS. 13-15. *Gnathodus mononodosus* sp. nov.

13a. Lateral view of paratype X 126. 13b. Lateral view of paratype X 126. 13c. Oral view of paratype X 126. 13d. Aboral view of paratype X 126. 14a. Lateral view of holotype X 124. 14b. Lateral view of holotype X 124. 14c. Aboral view of holotype X 124. 14d. Oral view of holotype X 124. 15a. Lateral view of paratype X 125. 15b. Lateral view of paratype X 125. 15c. Aboral view of paratype X 125. 15d. Oral view of paratype X 125.

FIGS. 16-20. *Gnathodus nodosus* Bischoff

16a. Lateral view of specimen X 128. 16b. Lateral view of specimen X 128. 16c. Aboral view of specimen X 128. 16d. Oral view of specimen X 128. 17a. Lateral view of specimen X 509. 17b. Lateral view of specimen X 509. 17c. Aboral view of specimen X 509. 17d. Oral view of specimen X 509. 18a. Lateral view of specimen X 510. 18b. Lateral view of specimen X 510. 18c. Aboral view of specimen X 510. 18d. Oral view of specimen X 510. 19a. Lateral view of specimen X 129. 19b. Lateral view of specimen X 129. 19c. Aboral view of specimen X 129. 19d. Oral view of specimen X 129. 20a. Lateral view of specimen X 127. 20b. Aboral view of specimen X 127. 20c. Oral view of specimen X 127.

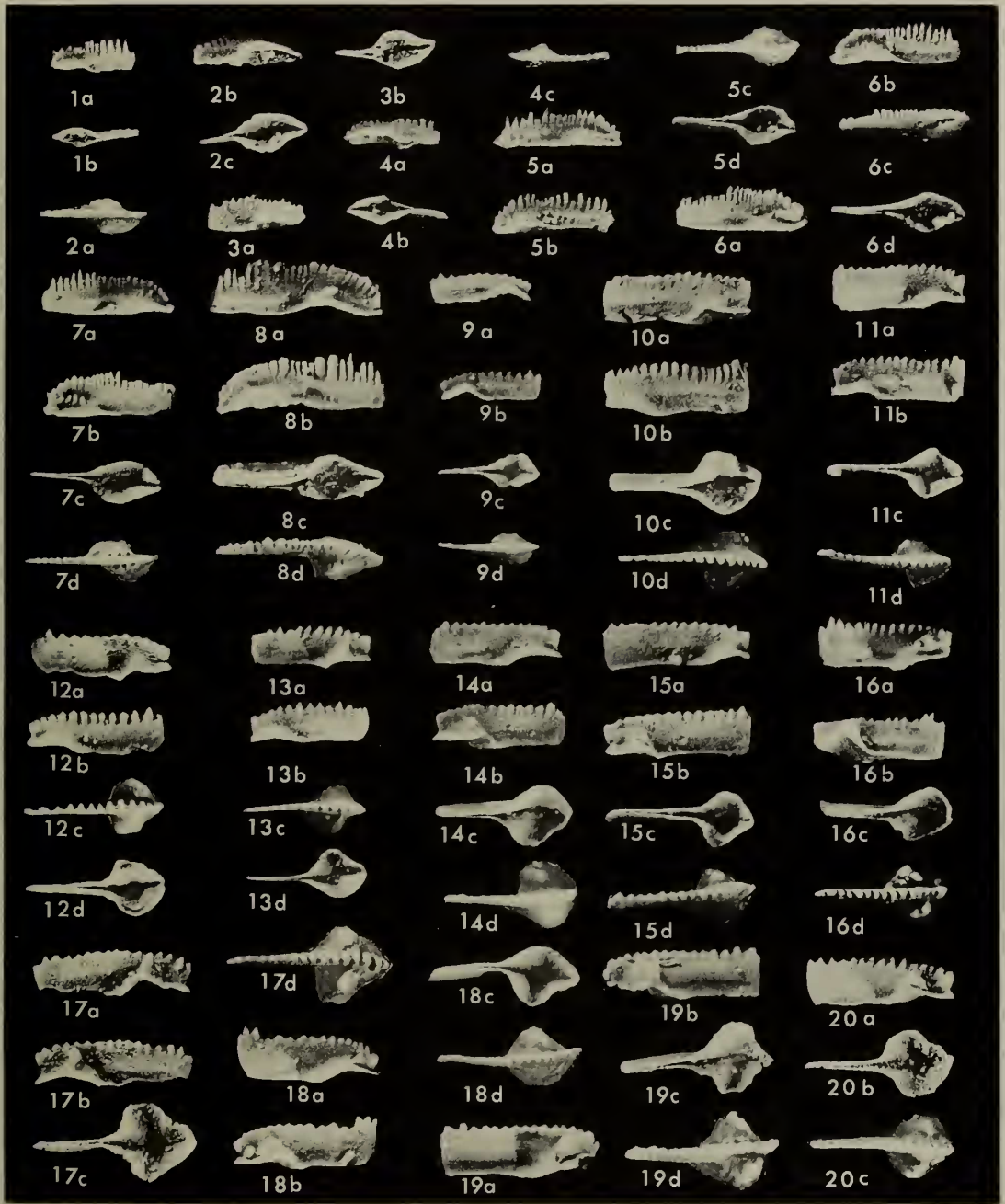


PLATE 20

All specimens coated and magnified $\times 31.5$

FIGS. 1-2. *Apatognathus chauliodus* Varker

1a. Inner lateral view of specimen X 44. 1b. Outer lateral view of specimen X 44. 2a. Inner lateral view of specimen X 550. 2b. Outer lateral view of specimen X 550.

FIGS. 3, 4, 6, 7. *Apatognathus geminus* (Hinde)

3a. Inner lateral view of specimen X 55. 3b. Outer lateral view of specimen X 55. 4a. Inner lateral view of specimen X 54. 4b. Outer lateral view of specimen X 54. 6a. Outer lateral view of specimen X 56. 6b. Inner lateral view of specimen X 56. 7a. Inner lateral view of specimen X 57. 7b. Outer lateral view of specimen X 57.

FIG. 5. *Apatognathus varians* Branson & Mehl

a. Inner lateral view of specimen X 42. b. Outer lateral view of specimen X 42.

FIG. 8. *Apatognathus cf. libratus* Varker

a. Inner lateral view of specimen X 58. b. Outer lateral view of specimen X 58.

FIGS. 9-11. *Apatognathus scalenus* Varker

9a. Inner lateral view of specimen X 48. 9b. Outer lateral view of specimen X 48. 10a. Inner lateral view of specimen X 49. 10b. Outer lateral view of specimen X 49. 11a. Inner lateral view of specimen X 47. 11b. Outer lateral view of specimen X 47.

FIGS. 12-14, 17. *Apatognathus petilus* Varker

12a. Outer lateral view of specimen X 51. 12b. Inner lateral view of specimen X 51. 13a. Inner lateral view of specimen X 52. 13b. Outer lateral view of specimen X 52. 14a. Inner lateral view of specimen X 50. 14b. Outer lateral view of specimen X 50. 17a. Inner lateral view of specimen X 53. 17b. Outer lateral view of specimen X 53.

FIGS. 15-16. *Apatognathus bladus* sp. nov.

15a. Inner lateral view of paratype X 46. 15b. Outer lateral view of paratype X 46. 16a. Inner lateral view of holotype X 45. 16b. Outer lateral view of holotype X 45.

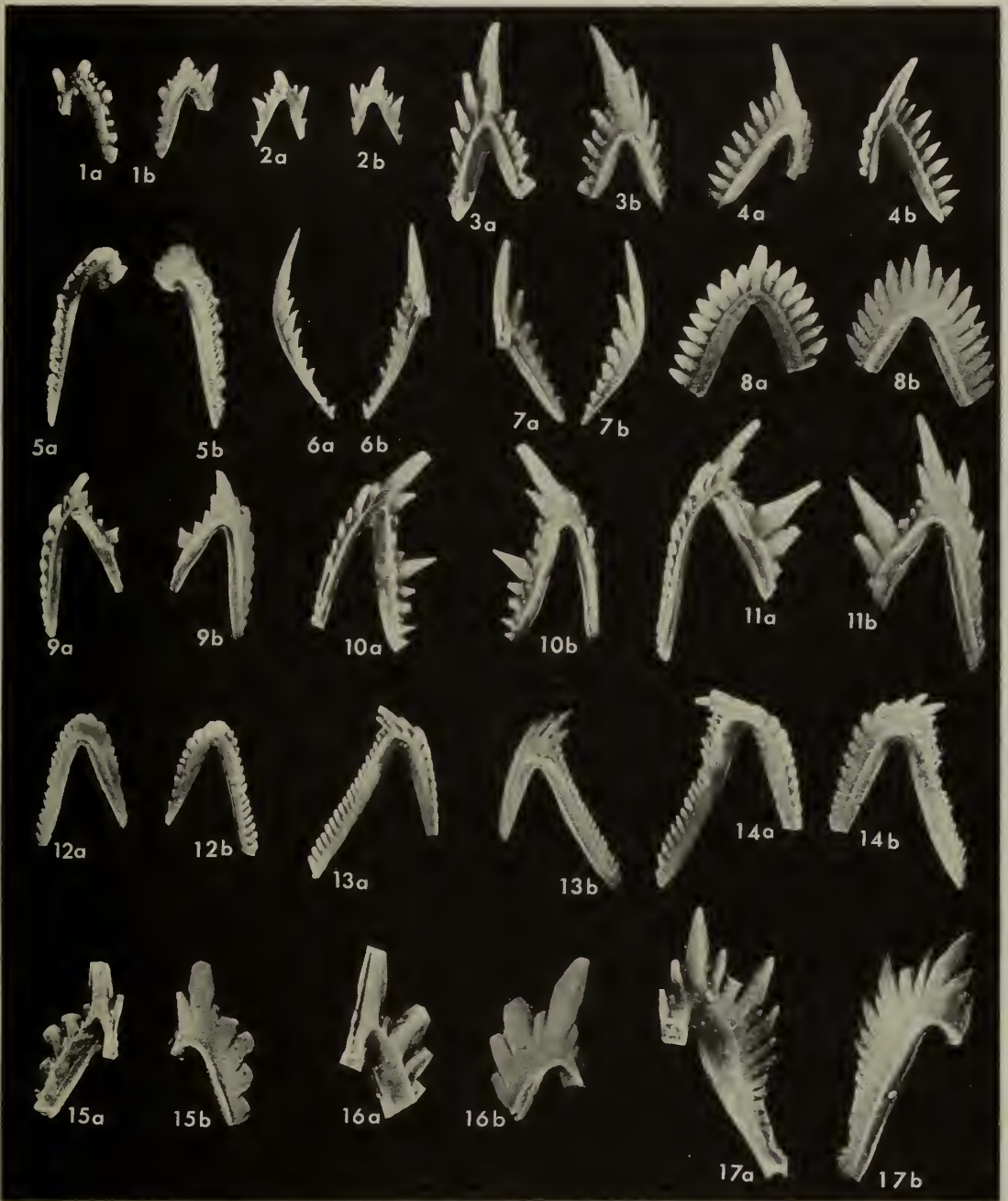


PLATE 21

All specimens coated and magnified $\times 31.5$

FIG. 1. *Neoprioniodus* cf. *confluens* (Branson & Mehl)

a. Lateral view of specimen X 520. b. Aboral view of specimen X 520. c. Oral view of specimen X 520.

FIGS. 2, 8. *Neoprioniodus confluens* (Branson & Mehl)

2a. Outer lateral view of specimen X 264. 2b. Inner lateral view of specimen X 264. 8a. Inner lateral view of specimen X 263. 8b. Outer lateral view of specimen X 263.

FIG. 3. *Neoprioniodus* cf. *armatus* (Hinde)

a. Inner lateral view of specimen X 283. b. Aboral view of specimen X 283. c. Oral view of specimen X 283.

FIGS. 4-7. *Neoprioniodus barbatus* (Branson & Mehl)

4. Lateral view of specimen X 259. 5a. Lateral view of specimen X 260. 5b. Aboral view of specimen X 260. 6. Lateral view of specimen X 262. 7. Lateral view of specimen X 261.

FIG. 9. *Neoprioniodus spathatus* Higgins

a. Outer lateral view of specimen X 279. b. Inner lateral view of specimen X 279.

FIGS. 10-11. *Neoprioniodus antespithatus* Collinson and Druce

10a. Outer lateral view of specimen X 258. 10b. Inner lateral view of specimen X 258. 11a. Inner lateral view of specimen X 257. 11b. Outer lateral view of specimen X 257.

FIGS. 12-15. *Neoprioniodus peracutus* (Hinde)

12a. Inner lateral view of specimen X 273. 12b. Outer lateral view of specimen X 273. 13a. Outer lateral view of specimen X 275. 13b. Inner lateral view of specimen X 275. 14a. Inner lateral view of specimen X 274. 14b. Outer lateral view of specimen X 274. 15a. Outer lateral view of specimen X 272. 15b. Inner lateral view of specimen X 272.

FIGS. 16, 17, 20. *Neoprioniodus conjunctus* (Gunnell)

16a. Inner lateral view of specimen X 265. 16b. Outer lateral view of specimen X 265. 17a. Outer lateral view of specimen X 266. 17b. Inner lateral view of specimen X 266. 20a. Inner lateral view of specimen X 267. 20b. Outer lateral view of specimen X 267.

FIG. 18. *Neoprioniodus varians* (Branson & Mehl)

a. Outer lateral view of specimen X 281. b. Inner lateral view of specimen X 281.

FIG. 19. *Neoprioniodus tulensis* (Pander)

a. Outer lateral view of specimen X 280. b. Inner lateral view of specimen X 280.

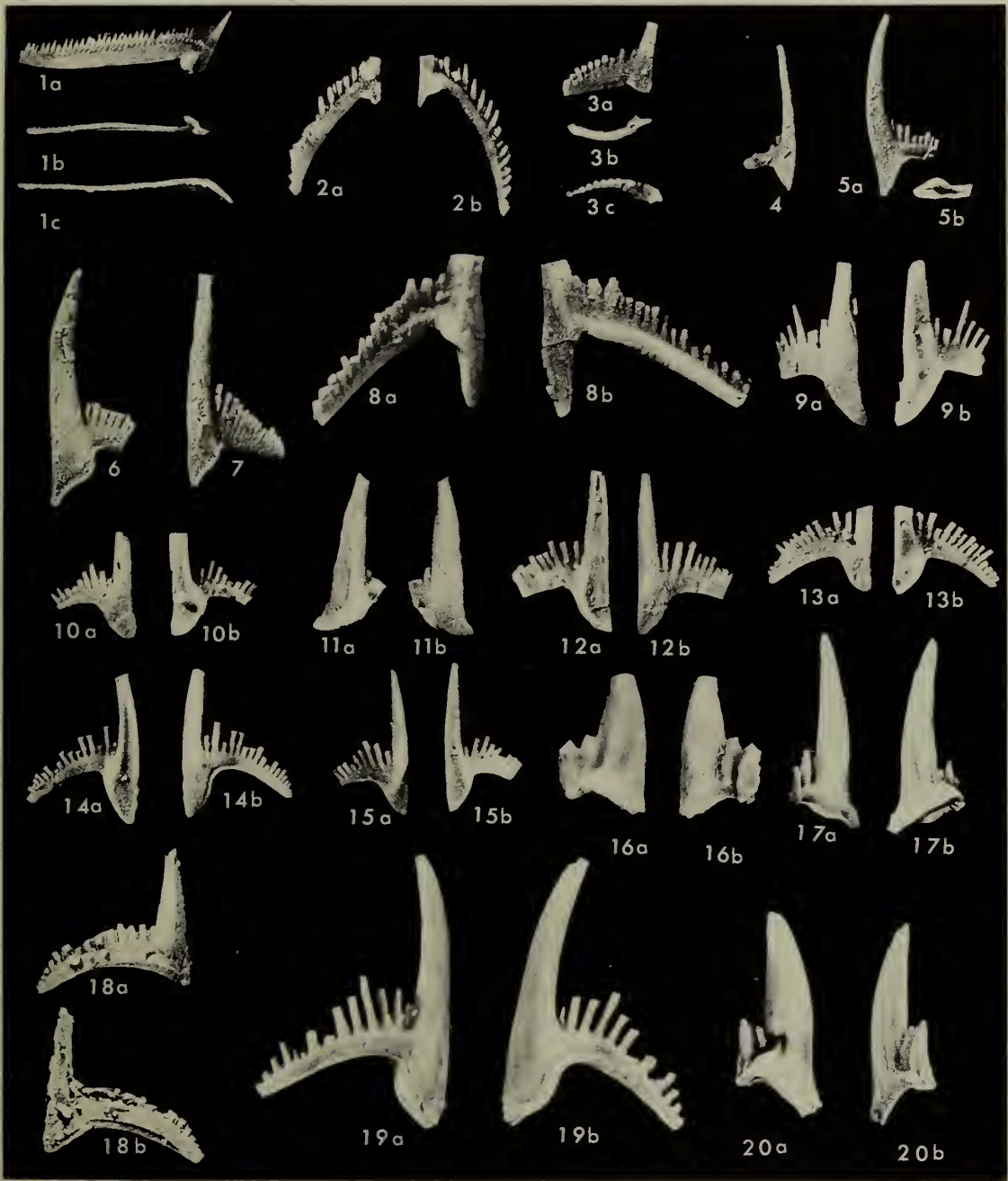


PLATE 22

All specimens coated and magnified $\times 31.5$

FIGS. 1-4. *Neoprioniodus* cf. *camurus* Rexroad

1a. Inner lateral view of specimen X 285. 1b. Outer lateral view of specimen X 285. 2a. Inner lateral view of specimen X 287. 2b. Outer lateral view of specimen X 287. 3a. Inner lateral view of specimen X 284. 3b. Outer lateral view of specimen X 284. 4a. Inner lateral view of specimen X 286. 4b. Outer lateral view of specimen X 286.

FIGS. 5-8. *Neoprioniodus montanaensis* (Scott)

5a. Outer lateral view of specimen X 271. 5b. Inner lateral view of specimen X 271. 6a. Inner lateral view of specimen X 269. 6b. Outer lateral view of specimen X 269. 7a. Outer lateral view of specimen X 268. 7b. Inner lateral view of specimen X 268. 8a. Outer lateral view of specimen X 270. 8b. Inner lateral view of specimen X 270.

FIGS. 9, 10, 12. *Neoprioniodus scitulus* (Branson & Mehl)

9a. Lateral view of specimen X 277. 9b. Lateral view of specimen X 277. 10a. Lateral view of specimen X 276. 10b. Lateral view of specimen X 276. 12a. Lateral view of specimen X 278. 12b. Lateral view of specimen X 278.

FIG. 11. *Euprioniodina caverna* (Collinson & Druce)

a. Outer lateral view of specimen X 83. b. Inner lateral view of specimen X 83.

FIG. 13. *Euprioniodina* sp. nov. A

a. Inner lateral view of specimen X 86. b. Outer lateral view of specimen X 86.

FIG. 14. *Neoprioniodus* sp. nov. A

Inner lateral view of specimen X 282.

FIG. 15. *Euprioniodina* sp.

a. Inner lateral view of specimen X 85. b. Outer lateral view of specimen X 85.

FIG. 16. *Euprioniodina microdentata* (Ellison)

a. Inner lateral view of specimen X 84. b. Outer lateral view of specimen X 84.

FIG. 17-20. *Hindeodus* sp.

17a. Outer lateral view of specimen X 191. 17b. Inner lateral view of specimen X 191. 18a. Outer lateral view of specimen X 189. 18b. Inner lateral view of specimen X 189. 19a. Outer lateral view of specimen X 188. 19b. Inner lateral view of specimen X 188. 20a. Inner lateral view of specimen X 190. 20b. Outer lateral view of specimen X 190.

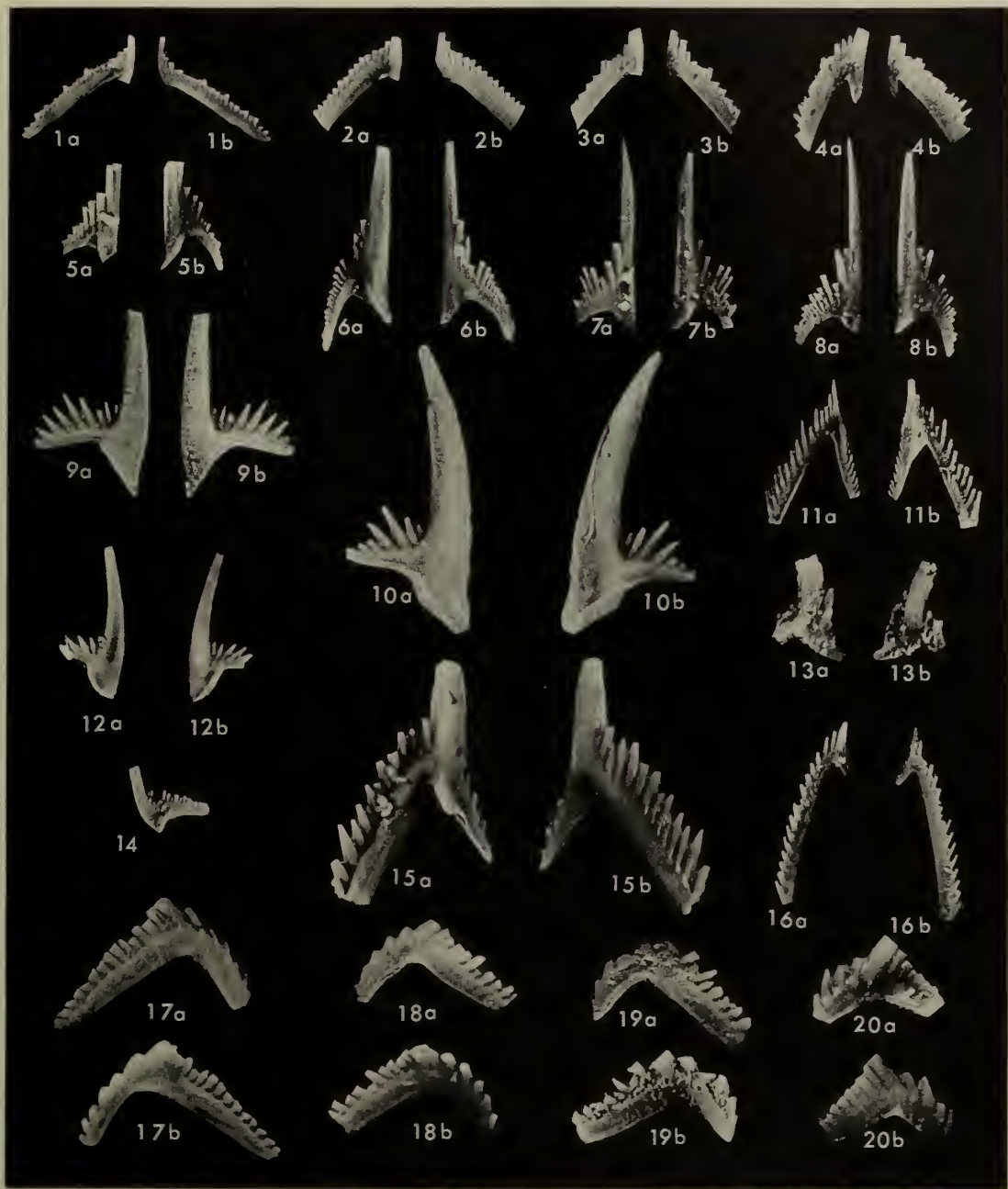


PLATE 23

All specimens coated and magnified $\times 31.5$

FIGS. 1-2. *Kladognathus clarensis* Collinson and Druce

1a. Outer lateral view of specimen X 196. 1b. Inner lateral view of specimen X 196. 2a. Inner lateral view of specimen X 195. 2b. Outer lateral view of specimen X 195.

FIGS. 3-6. *Kladognathus macrodentatus* (Higgins)

3a. Inner lateral view of specimen X 197. 3b. Outer lateral view of specimen X 197. 3c. Oral view of specimen X 197. 4a. Inner lateral view of specimen X 198. 4b. Outer lateral view of specimen X 198. 4c. Oral view of specimen X 198. 5a. Outer lateral view of specimen X 199. 5b. Inner lateral view of specimen X 199. 5c. Oral view of specimen X 199. 6a. Inner lateral view of specimen X 200. 6b. Outer lateral view of specimen X 200. 6c. Oral view of specimen X 200.

FIG. 7. *Magnilaterella* ? sp.

a. Inner lateral view of specimen X 447. b. Outer lateral view of specimen X 447.

FIGS. 8, 18. *Magnilaterella contraria* sp. nov.

8a. Inner lateral view of holotype X 553. 8b. Aboral view of holotype X 553. 8c. Outer lateral view of holotype X 553. 18a. Outer lateral view of paratype X 517. 18b. Inner lateral view of paratype X 517. 18c. Aboral view of paratype X 517.

FIG. 9, 10. *Magnilaterella* spp.

9. Inner lateral view of specimen X 244. 10. Inner lateral view of specimen X 242.

FIGS. 11-13. *Magnilaterella clarkei* sp. nov.

11. Inner lateral view of paratype X 241. 12. Inner lateral view of holotype X 431. 13a. Outer lateral view of paratype X 432. 13b. Inner lateral view of paratype X 432.

FIGS. 14-17. *Magnilaterella complectens* (Clarke)

14a. Outer lateral view of specimen X 238. 14b. Aboral view of specimen X 238. 14c. Inner lateral view of specimen X 238. 15a. Inner lateral view of specimen X 239. 15b. Aboral view of specimen X 239. 15c. Outer lateral view of specimen X 239. 16a. Outer lateral view of specimen X 240. 16b. Aboral view of specimen X 240. 16c. Inner lateral view of specimen X 240. 17a. Outer lateral view of specimen X 237. 17b. Inner lateral view of specimen X 237. 17c. Aboral view of specimen X 237.

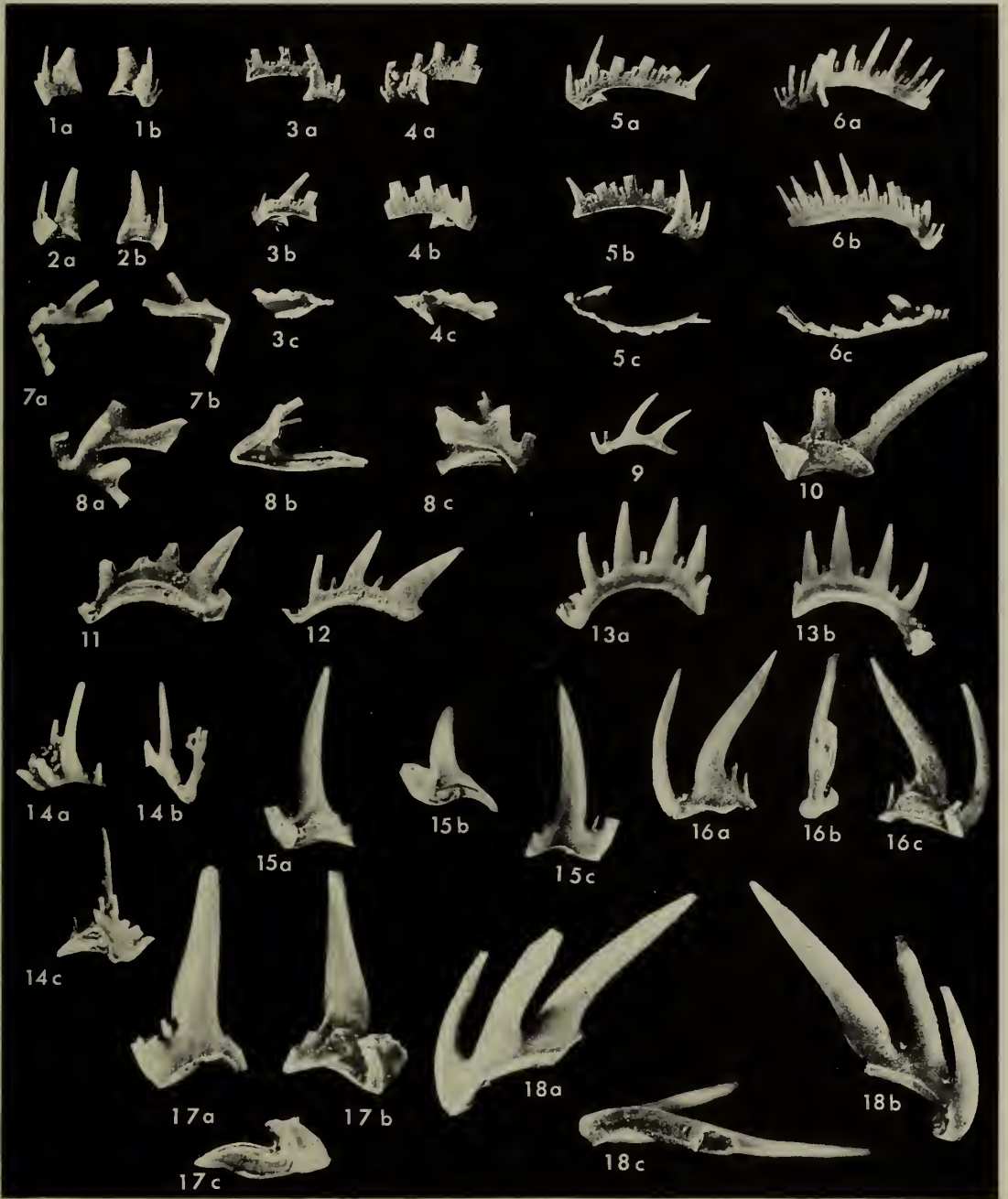


PLATE 24

All specimens coated and magnified $\times 31.5$

FIGS. 1-6. *Prioniodina prelaevipostica* sp. nov.

1. Inner lateral view of paratype X 333. 2. Inner lateral view of paratype X 332. 3a. Inner lateral view of paratype X 331. 3b. Oral view of paratype X 331. 3c. Aboral view of paratype X 331. 4a. Inner lateral view of holotype X 334. 4b. Oral view of holotype X 334. 4c. Aboral view of holotype X 334. 5. Inner lateral view of paratype X 335. 6. Inner lateral view of paratype X 336.

FIG. 7. *Lonchodina obtunda* Collinson & Druce

a. Inner lateral view of specimen X 229. b. Oral view of specimen X 229. c. Aboral view of specimen X 229.

FIGS. 8-11. *Metalonchodina bidentata* (Gunnell)

8a. Outer lateral view of specimen X 256. 8b. Inner lateral view of specimen X 256. 9a. Inner lateral view of specimen X 253. 9b. Outer lateral view of specimen X 253. 9c. Aboral view of specimen X 253. 10a. Inner lateral view of specimen X 254. 10b. Outer lateral view of specimen X 254. 11a. Outer lateral view of specimen X 255. 11b. Inner lateral view of specimen X 255.

FIGS. 12-14. *Lonchodina bolbosa* Collinson & Druce

12a. Oral view of specimen X 223. 12b. Aboral view of specimen X 223. 13a. Oral view of specimen X 222. 13b. Aboral view of specimen X 222. 13c. Lateral view of specimen X 222. 14a. Oral view of specimen X 224. 14b. Aboral view of specimen X 224.

FIGS. 15, 18. *Lonchodina paraclaviger* Rexroad

15a. Aboral view of specimen X 233. 15b. Oral view of specimen X 233. 18a. Oral view of specimen X 232. 18b. Aboral view of specimen X 232.

FIG. 16. *Lonchodina paraclarki* Hass

a. Aboro-lateral view of specimen X 231. b. Inner lateral view of specimen X 231.

FIG. 17. *Lonchodina* sp. A

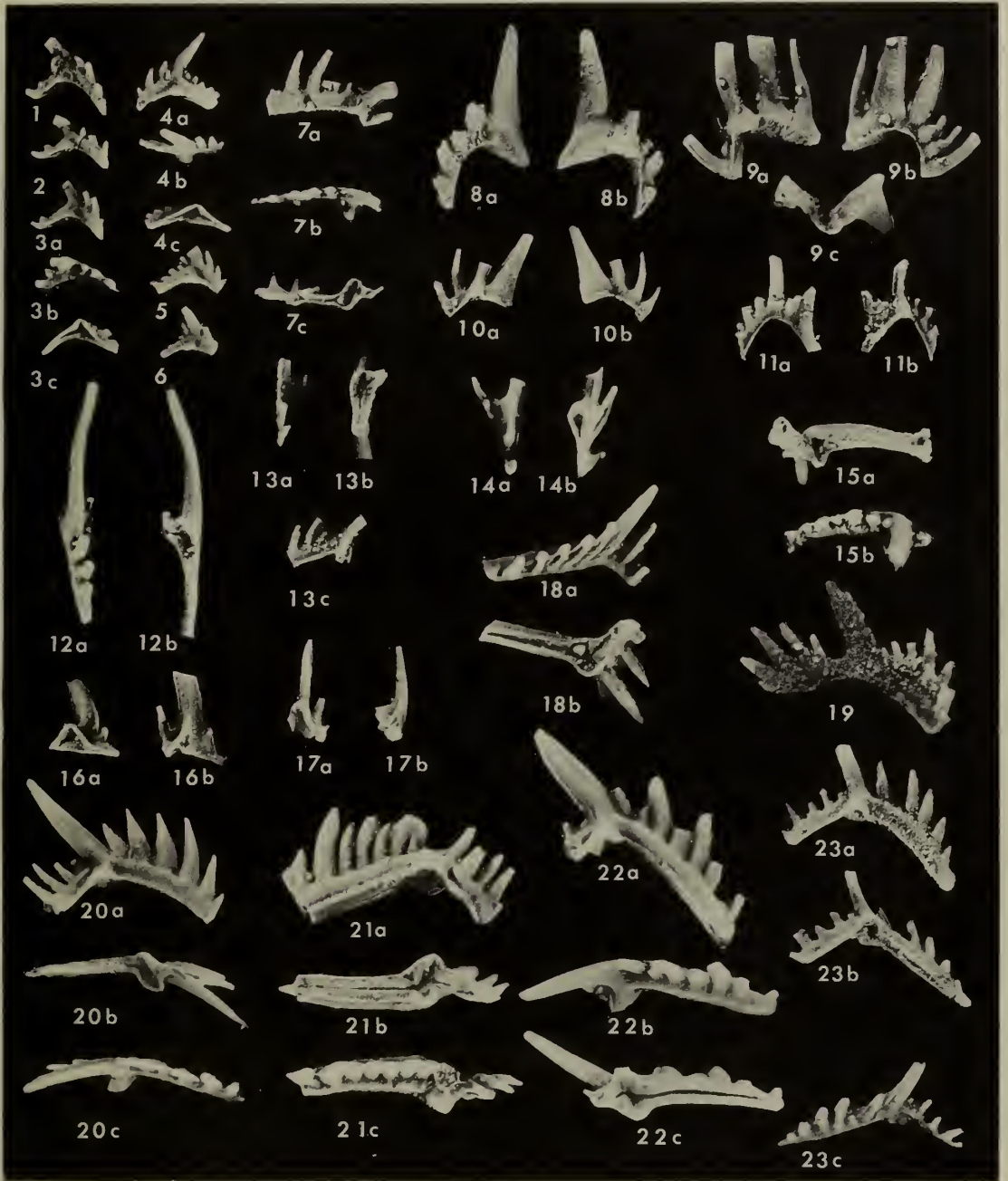
a. Aboro-lateral view of specimen X 424. b. Oral view of specimen X 424.

FIG. 19. *Prioniodina latericrescens* (Branson & Mehl)

Inner lateral view of specimen X 429.

FIGS. 20-23. *Lonchodina furnishi* Rexroad

20a. Inner lateral view of specimen X 227. 20b. Aboral view of specimen X 227. 20c. Oral view of specimen X 227. 21a. Lateral view of specimen X 226. 21b. Aboral view of specimen X 226. 21c. Oral view of specimen X 226. 22a. Lateral view of specimen X 225. 22b. Oral view of specimen X 225. 22c. Aboral view of specimen X 225. 23a. Lateral view of specimen X 228. 23b. Aboro-lateral view of specimen X 228. 23c. Oral view of specimen X 228.



All specimens coated and magnified $\times 31.5$

FIG. 1. *Hibbardella (Roundya)* sp.

Lateral view of specimen X 423.

FIGS. 2-5. *Hibbardella (Roundya) barnettana* Hass

2a. Aboro-lateral view of specimen X 154. 2b. Lateral view of specimen X 154. 3a. Anterior view of specimen X 152. 3b. Posterior view of specimen X 152. 4a. Postero-lateral view of specimen X 151. 4b. Lateral view of specimen X 151. 5a. Lateral view of specimen X 153. 5b. Aboral view of specimen X 153.

FIG. 6. Gen. nov. A sp.

a. Lateral view of specimen X 409. b. Oral view of specimen X 409.

FIG. 7. Gen. nov. B sp.

a. Lateral view of specimen X 410. b. Aboral view of specimen X 410.

FIGS. 8, 9. *Plectospathodus* ? sp. nov. A

8a. Inner lateral view of specimen X 313. 8b. Oral view of specimen X 313. 9. Inner lateral view of specimen X 312.

FIGS. 10-12. *Plectospathodus* ? sp. nov. B

10. Inner lateral view of specimen X 427. 11. Inner lateral view of specimen X 428. 12. Inner lateral view of specimen X 314.

FIGS. 13-14. *Hibbardella (Hassognathus) separata* (Branson & Mehl)

13a. Lateral view of specimen X 150. 13b. Aboral view of specimen X 150. 13c. Posterior view of specimen X 150. 14. Lateral view of specimen X 149.

FIG. 15. *Hibbardella (Hibbardella)* sp.

a. Posterior view of specimen X 441. b. Anterior view of specimen X 441.

FIGS. 16-18. *Hibbardella (Hibbardella)* cf. *macrodentata* Thomas

16a. Posterior view of specimen X 147. 16b. Oral view of specimen X 147. 17a. Lateral view of specimen X 146. 17b. Posterior view of specimen X 146. 18a. Lateral view of specimen X 148. 18b. Oral view of specimen X 148. 18c. Posterior view of specimen X 148.

FIGS. 19-20. *Hibbardella (Hibbardella) acuta* Murray & Chronic

19a. Posterior view of specimen X 139. 19b. Anterior view of specimen X 139. 20. Lateral view of specimen X 422.

FIG. 21. *Hibbardella (Hibbardella) parva* sp. nov.

a. Anterior view of holotype X 144. b. Posterior view of holotype X 144.

FIG. 22. *Hibbardella (Hibbardella) ortha* Rexroad

a. Posterior view of specimen X 143. b. Anterior view of specimen X 143.

FIGS. 23-25. *Hibbardella (Hibbardella) milleri* Rexroad

23a. Anterior view of specimen X 140. 23b. Posterior view of specimen X 140. 24a. Anterior view of specimen X 141. 24b. Aboral view of specimen X 141. 24c. Posterior view of specimen X 141. 25a. Anterior view of specimen X 142. 25b. Posterior view of specimen X 142.

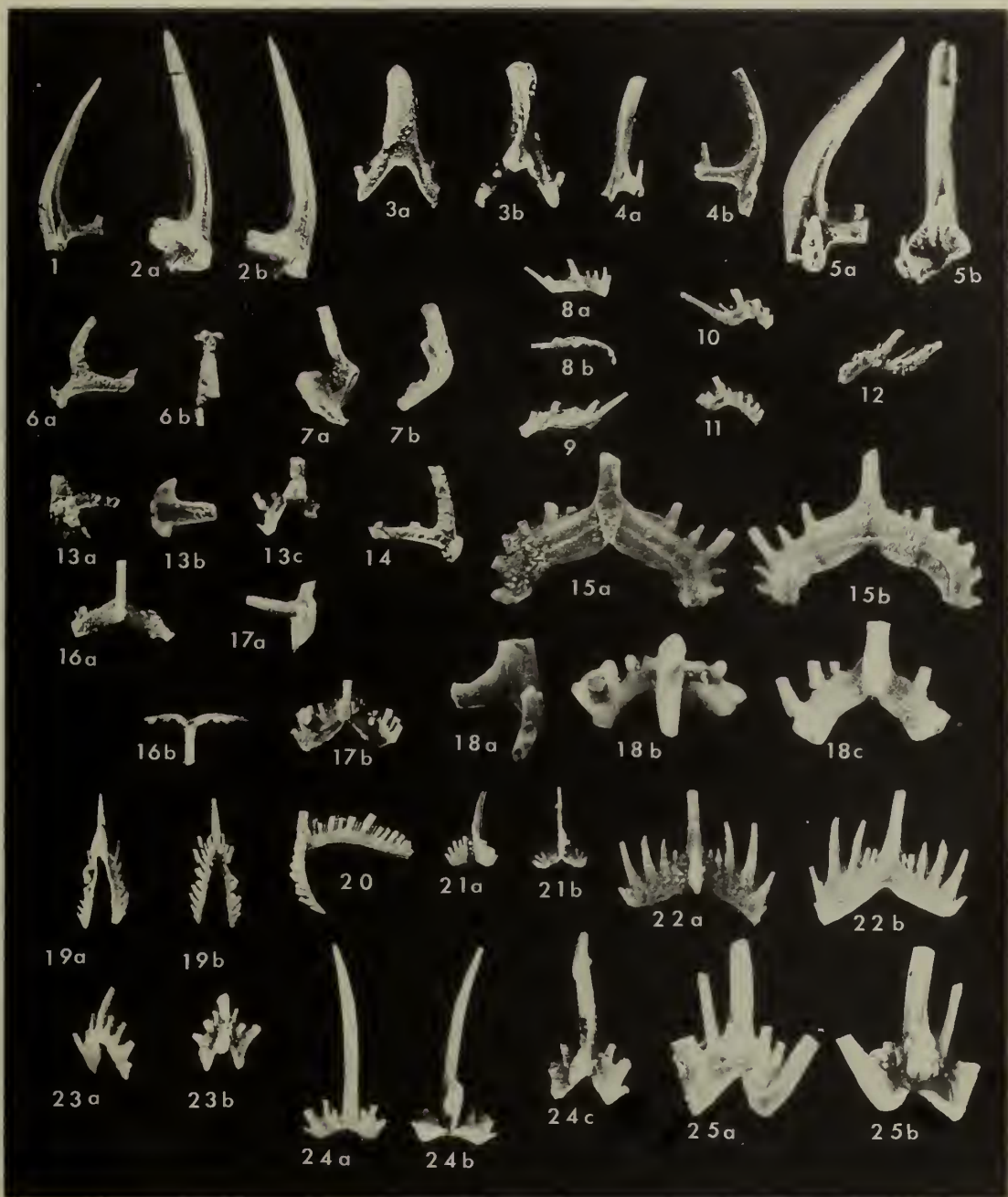


PLATE 26

All specimens coated and magnified $\times 31.5$

FIGS. 1-2. *Ligonodina osborni* sp. nov.

1a. Outer lateral view of holotype X 212. 1b. Posterior view of holotype X 212. 1c. Inner lateral view of holotype X 212. 2a. Outer lateral view of paratype X 213. 2b. Posterior view of paratype X 213. 2c. Inner lateral view of paratype X 213.

FIG. 3. *Ligonodina* sp. A

3a. Inner lateral view of specimen X 217. 3b. Oral view of specimen X 217. 3c. Aboral view of specimen X 217.

FIGS. 4-6. *Ligonodina beata* nom. nov.

4. Inner lateral view of specimen X 203. 5a. Inner lateral view of specimen X 201. 5b. Oral view of specimen X 201. 5c. Aboral view of specimen X 201. 6a. Inner lateral view of specimen X 202. 6b. Aboral view of specimen X 202.

FIG. 7. *Ligonodina* ? sp.

Inner lateral view of specimen X 218.

FIGS. 8-11. *Ligonodina magnilaterina* sp. nov.

8a. Inner lateral view of paratype X 210. 8b. Outer lateral view of paratype X 210. 9a. Outer lateral view of paratype X 208. 9b. Inner lateral view of paratype X 208. 10a. Inner lateral view of paratype X 209. 10b. Outer lateral view of paratype X 209. 11a. Outer lateral view of holotype X 211. 11b. Inner lateral view of holotype X 211.

FIG. 12. *Ligonodina* ? sp.

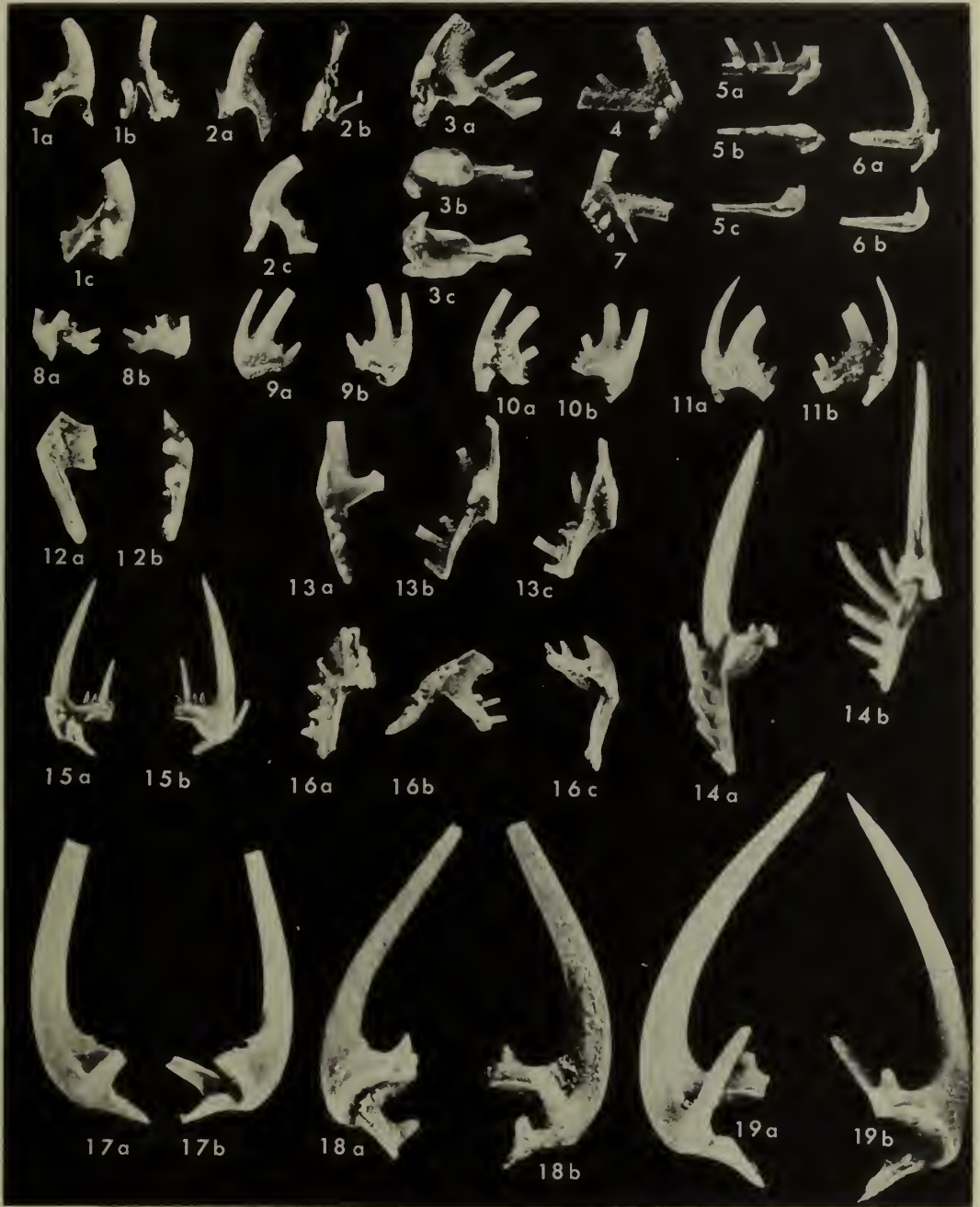
a. Aboral view of specimen X 219. b. Inner lateral view of specimen X 219.

FIGS. 13, 14, 16. *Ligonodina roundyi* Hass

13a. Inner lateral view of specimen X 216. 13b. Posterior view of specimen X 216. 13c. Aboral view of specimen X 216. 14a. Postero-lateral view of specimen X 214. 14b. Posterior view of specimen X 214. 16a. Posterior view of specimen X 215. 16b. Inner lateral view of specimen X 215. 16c. Aboral view of specimen X 215.

FIGS. 15, 17-19. *Ligonodina levis* Branson & Mehl

15a. Inner lateral view of specimen X 207. 15b. Outer lateral view of specimen X 207. 17a. Inner lateral view of specimen X 206. 17b. Outer lateral view of specimen X 206. 18a. Outer lateral view of specimen X 205. 18b. Inner lateral view of specimen X 205. 19a. Inner lateral view of specimen X 204. 19b. Outer lateral view of specimen X 204.



All specimens coated and magnified $\times 31.5$

FIGS. 1-3. *Ozarkodina plana* (Huddle)

1. Lateral view of specimen X 301. 2. Lateral view of specimen X 300. 3. Lateral view of specimen X 419.

FIGS. 4, 5. *Ozarkodina plumula* Collinson & Druce

4. Lateral view of specimen X 302. 5a. Lateral view of specimen X 303. 5b. Aboral lateral view of specimen X 303.

FIG. 6. *Ozarkodina curvata* Rexroad

- a. Outer lateral view of specimen X 289. b. Inner lateral view of specimen X 289.

FIGS. 7, 8. *Ozarkodina macer* (Branson & Mehl)

7. Lateral view of specimen X 305. 8. Lateral view of specimen X 304.

FIGS. 9-11. *Ozarkodina* sp.

9. Lateral view of specimen X 307. 10. Lateral view of specimen X 308. 11. Lateral view of specimen X 306.

FIGS. 12, 20, 21. *Ozarkodina macra* Branson & Mehl

12. Lateral view of specimen X 297. 20. Lateral view of specimen X 296. 21. Lateral view of specimen X 298.

FIG. 13. *Ozarkodina* cf. *congesta* Stauffer

Lateral view of specimen X 288.

FIG. 14. *Ozarkodina* cf. *delicatula* (Stauffer & Plummer)

- a. Lateral view of specimen X 292. b. Oral view of specimen X 292.

FIGS. 15, 19. *Ozarkodina delicatula* (Stauffer & Plummer)

- 15a. Lateral view of specimen X 290. 15b. Oral view of specimen X 290. 15c. Aboral view of specimen X 290. 19a. Lateral view of specimen X 291. 19b. Oral view of specimen X 291. 19c. Aboral view of specimen X 291.

FIGS. 16, 17, 22. *Ozarkodina hindei* Clarke

16. Lateral view of specimen X 294. 17a. Outer lateral view of specimen X 293. 17b. Inner lateral view of specimen X 293. 22a. Aboral lateral view of specimen X 295. 22b. Lateral view of specimen X 295.

FIG. 18. *Ozarkodina parva* (Huddle)

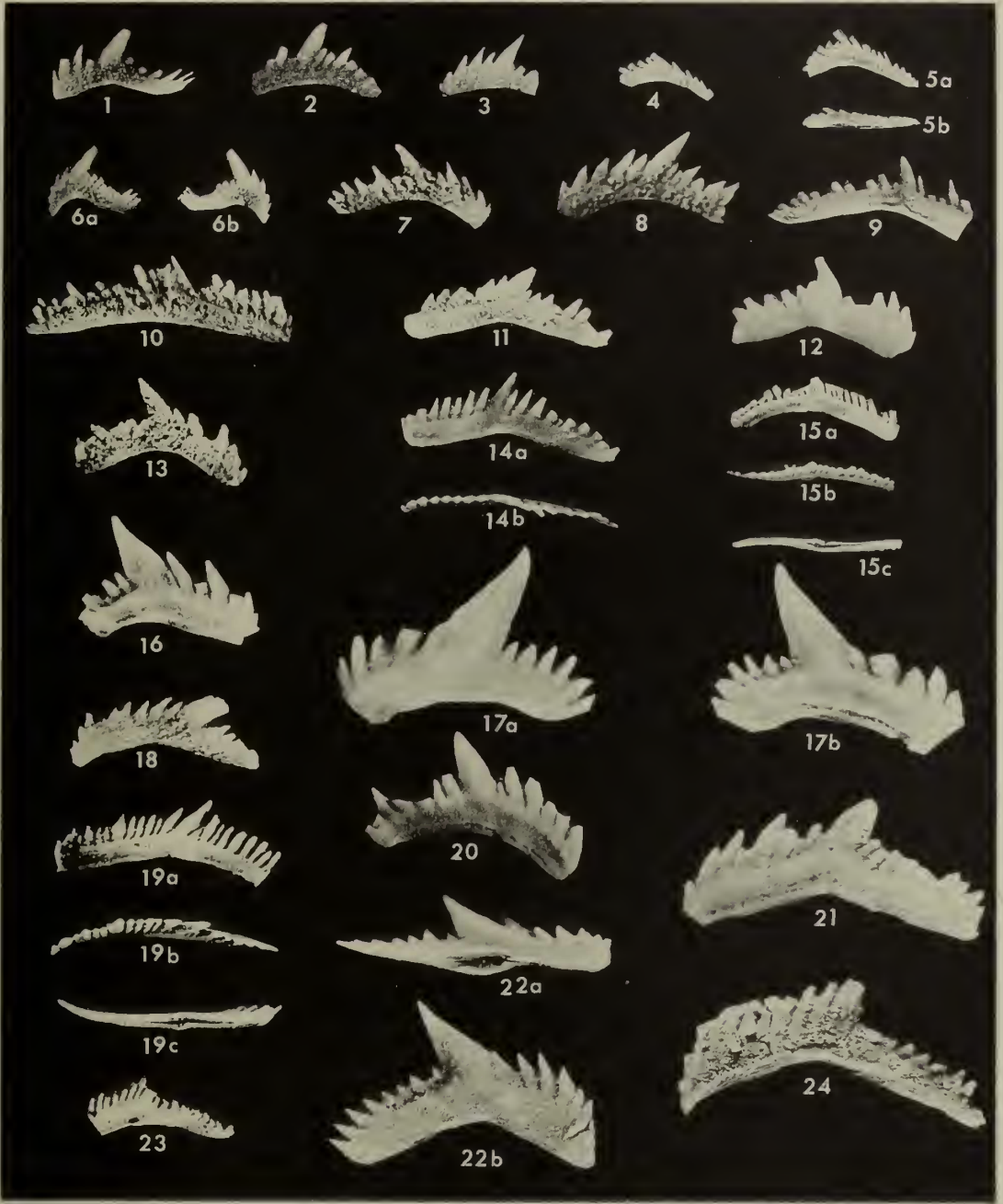
Lateral view of specimen X 299.

FIG. 23. *Ozarkodina compressa* Rexroad

Lateral view of specimen X 420.

FIG. 24. *Ozarkodina* cf. *elegans* (Stauffer)

Lateral view of specimen X 109.



All specimens coated and magnified $\times 31.5$ FIGS. 1-4. *Prioniodina subaequalis* (Higgins)

1a. Lateral view of specimen X 344. 1b. Aboral view of specimen X 344. 1c. Oral view of specimen X 344. 2a. Lateral view of specimen X 343. 2b. Oral view of specimen X 343. 3a. Aboral view of specimen X 341. 3b. Lateral view of specimen X 341. 3c. Oral view of specimen X 341. 4. Lateral view of specimen X 342.

FIG. 5. *Prioniodina oweni* sp. nov.

a. Lateral view of holotype X 330. b. Oral view of holotype X 330. c. Aboral view of holotype X 330.

FIG. 6. *Prioniodina* ? sp. nov.

a. Lateral view of holotype X 345. b. Aboral view of holotype X 345. c. Oral view of holotype X 345.

FIGS. 7-10. *Prioniodina stipans* (Rexroad)

7a. Lateral view of specimen X 338. 7b. Aboral view of specimen X 338. 7c. Oral view of specimen X 338. 8a. Lateral view of specimen X 337. 8b. Aboral view of specimen X 337. 8c. Oral view of specimen X 337. 9a. Lateral view of specimen X 339. 9b. Aboral view of specimen X 339. 9c. Oral view of specimen X 339. 10a. Lateral view of specimen X 340. 10b. Aboral view of specimen X 340. 10c. Oral view of specimen X 340.

FIGS. 11-12. *Prioniodina laevipostica* (Rexroad & Collinson)

11. Inner lateral view of specimen X 317. 12a. Outer lateral view of specimen X 316. 12b. Inner lateral view of specimen X 316.

FIG. 13. *Prioniodina eireica* (Collinson & Druce)

Inner lateral view of specimen X 315.

FIG. 14. *Hindeodella* sp. nov.

a. Oral view of specimen X 186. b. Lateral view of specimen X 186.

FIGS. 15-17. *Hindeodella croka* Collinson & Druce

15. Oral view of specimen X 164. 16. Oral view of specimen X 162. 17. Oral view of specimen X 163.

FIGS. 18-20. *Hindeodella hibbardi* Collinson & Druce

18. Lateral view of specimen X 167. 19. Lateral view of specimen X 168. 20. Lateral view of specimen X 169.

FIGS. 21, 26. *Hindeodella montanaensis* (Scott)

21. Lateral view of specimen X 175. 26. Lateral view of specimen X 176.

FIGS. 22-24, 30-31. *Hindeodella ibergensis* (Bischoff)

22. Lateral view of specimen X 171. 23. Lateral view of specimen X 170. 24. Lateral view of specimen X 173. 30. Lateral view of specimen X 172. 31. Lateral view of specimen X 174.

FIGS. 25, 28. *Hindeodella antecomplex* Collinson & Druce

25. Lateral view of specimen X 157. 28. Lateral view of specimen X 156.

FIG. 27. *Hindeodella tenuis* Clarke

Lateral view of specimen X 187.

FIG. 29. *Hindeodella* cf. *croka* Collinson & Druce

Oral view of specimen X 165

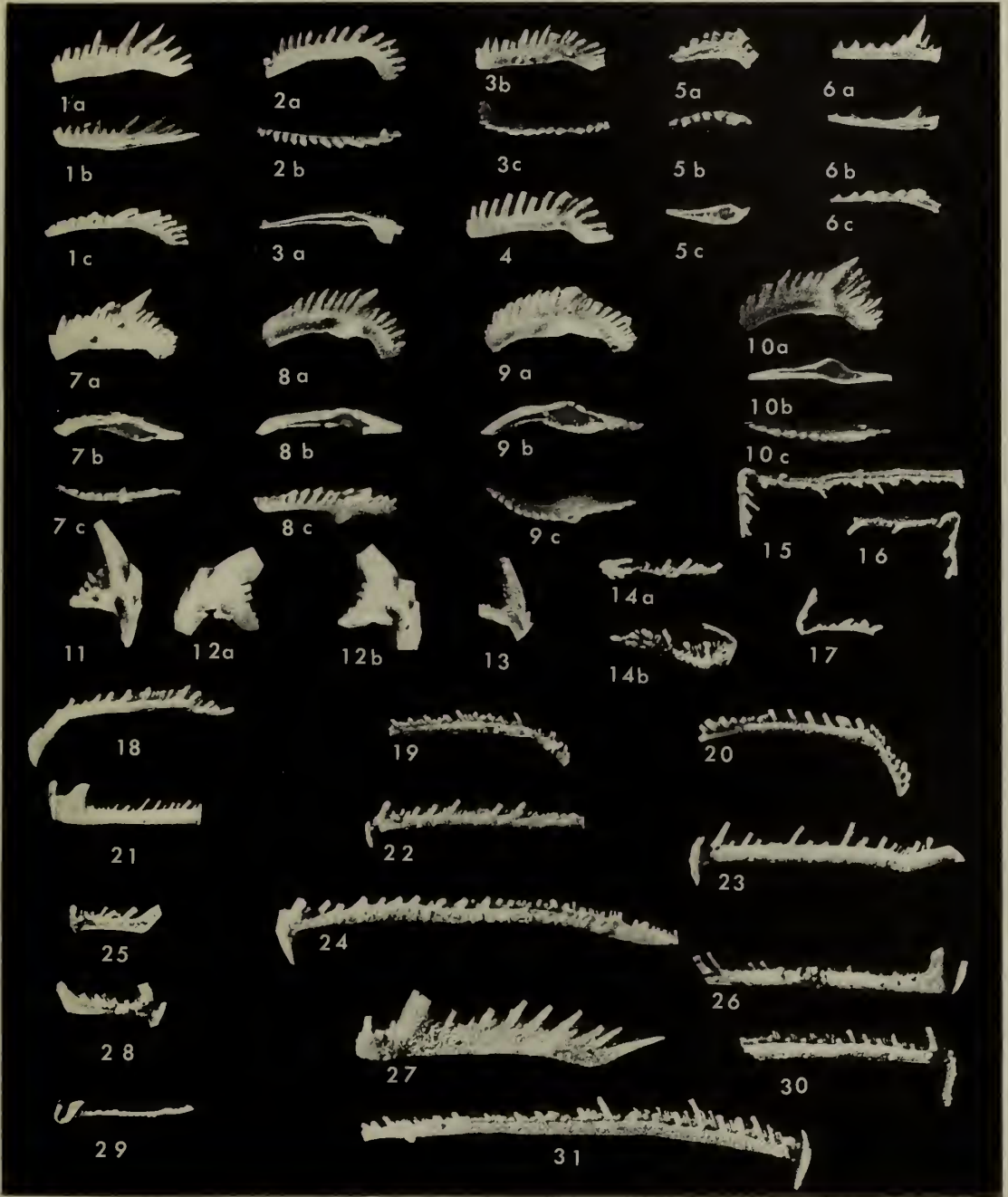


PLATE 29

All specimens coated and magnified $\times 31.5$

FIGS. 1-2. *Angulodus* sp. nov. D

1a. Lateral view of specimen X 41. 1b. Oral view of specimen X 41. 1c. Aboral view of specimen X 41. 2a. Lateral view of specimen X 40. 2b. Oral view of specimen X 40. 2c. Aboral view of specimen X 40.

FIGS. 3-4. *Angulodus* sp. nov. C.

3a. Lateral view of specimen X 39. 3b. Oral view of specimen X 39. 3c. Aboral view of specimen X 39. 4a. Lateral view of specimen X 38. 4b. Oral view of specimen X 38. 4c. Aboral view of specimen X 38.

FIG. 5. *Angulodus* sp. nov. B.

a. Lateral view of specimen X 37. b. Aboral view of specimen X 37.

FIGS. 6-7, 9-10. *Hindeodella subtilis* Ulrich & Bassler

6a. Lateral view of specimen X 180. 6b. Oral view of specimen X 180. 7a. Lateral view of specimen X 177. 7b. Oral view of specimen X 177. 9. Lateral view of specimen X 178. 10a. Lateral view of specimen X 179. 10b. Oral view of specimen X 179.

FIG. 8. *Angulodus walrathi* (Hibbard)

Lateral view of specimen X 36.

FIGS. 11, 13-15. *Hindeodella secarata* Collinson & Druce

11. Lateral view of specimen X 184. 13. Lateral view of specimen X 181. 14. Lateral view of specimen X 182. 15. Lateral view of specimen X 183.

FIG. 12. *Hindeodella* sp.

a. Lateral view of specimen X 445. b. Oral view of specimen X 445. c. Aboral view of specimen X 445.

FIGS. 16-17. *Hindeodella corpulenta* Branson & Mehl

16a. Lateral view of specimen X 160. 16b. Postero-lateral view of specimen X 160. 16c. Aboral view of specimen X 160. 17a. Aboral view of specimen X 161. 17b. Lateral view of specimen X 161. 17c. Postero-lateral view of specimen X 161.



PLATE 30

All specimens coated and magnified $\times 31.5$

FIG. 1. *Gnathodus semiglaber* Bischoff

a. Oral view of specimen X 421. b. Aboral view of specimen X 421. c. Lateral view of specimen X 421.

FIGS. 2, 8. *Gnathodus punctatus* – *Gnathodus semiglaber* transition

2. Oral view of specimen X 521. 8. Oral view of specimen X 525.

FIGS. 3, 7, 9–17. *Pseudopolygnathus* cf. *longiposticus* Branson & Mehl

3a. Aboral view of specimen X 443. 3b. Oral view of specimen X 443. 7a. Aboral lateral view of specimen X 448. 7b. Oral view of specimen X 448. 9. Aboral view of specimen X 442. 10. Oral view of specimen X 442. 11. Oral view of growth stages of specimen X 522. 12. Oral view of growth stages of specimen X 523. 13. Oral view of growth stages of specimen X 433. 14. Oral view of growth stages of specimen X 434. 15. Oral view of growth stages of specimen X 547. 16. Oral view of specimen X 449. 17a. Oral view of specimen X 545. 17b. Aboral view of specimen X 545.

FIGS. 4, 5. *Gnathodus* sp.

4a. Oral view of specimen X 424. 4b. Aboral view of specimen X 424. 4c. Lateral view of specimen X 424. 5a. Aboral view of specimen X 425. 5b. Oral view of specimen X 425. 5c. Lateral view of specimen X 425.

FIG. 6. *Gnathodus delicatus* Branson & Mehl

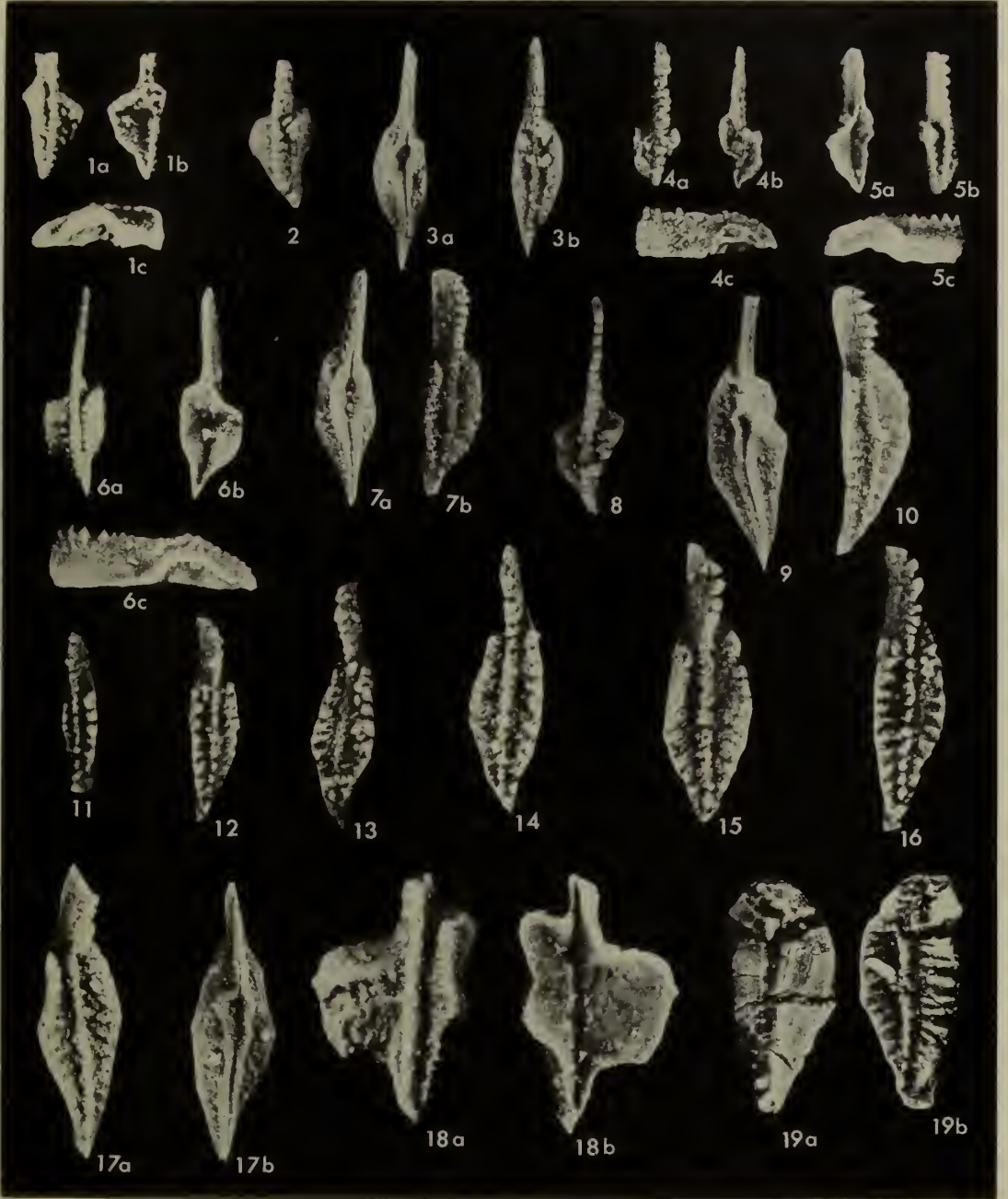
a. Oral view of specimen X 426. b. Aboral view of specimen X 426. c. Lateral view of specimen X 426.

FIG. 18. *Gnathodus bilineatus* (Roundy) transitional from *G. punctatus* (Cooper)

a. Oral view of specimen X 439. b. Aboral view of specimen X 439.

FIG. 19. *Pseudopolygnathus triangulus* cf. *pinnatus* Voges

a. Aboral view of specimen X 502. b. Oral view of specimen X 502.



All specimens coated and magnified $\times 31.5$

FIG. 1. *Hindeodella undata* Branson & Mehl
Lateral view of specimen X 185.

FIG. 2. *Apatognathus* sp.
Inner lateral view of specimen X 318.

FIG. 3. *Hibbardella (Hassognathus)* ? sp.
Lateral view of specimen X 319.

FIG. 4, 16. *Ligonodina tenuis* Branson & Mehl
4. Lateral view of specimen X 320. 16. Lateral view of specimen X 321.

FIGS. 5, 11. *Magnilaterella* spp.
5. Inner lateral view of specimen X 322. 11. Aboral inner lateral view of specimen X 323.

FIG. 6. *Hibbardella (Hibbardella) abnormis* Branson & Mehl
Lateral view of specimen X 508.

FIG. 7, 10. *Hindeodus alatoides* (Rexroad & Burton)
7. Lateral view of specimen X 193. 10. Lateral view of specimen X 192.

FIG. 8. *Hindeodus imperfectus* (Rexroad)
Lateral view of specimen X 194.

FIG. 9. *Ligonodina tulensis* (Pander)
Lateral view of specimen X 328.

FIG. 12. *Spathognathodus scitulus* subsp. nov.
a. Oral view of specimen X 390. b. Aboral view of specimen X 390. c. Lateral view of specimen X 390.

FIG. 13. *Cavusgnathus unicornis* Youngquist & Miller
a. Aboral view of specimen X 329. b. Lateral view of specimen X 329.

FIG. 14. *Lonchodina transitans* Collinson & Druce
Lateral view of specimen X 234.

FIG. 15. *Kladognathus mehli* (Rexroad)
Inner lateral view of specimen X 524.

FIG. 17. *Hindeodella brevis* Branson & Mehl
Lateral view of specimen X 514.

FIGS. 18, 19. *Hindeodella cooperi* (Elias)
18. Lateral view of specimen X 158. 19. Lateral view of specimen X 159.

FIG. 20. *Siphonodella* sp.
Oral view of specimen X 539.

FIG. 21. *Polygnathus* sp.
a. Oral view of specimen X 130. b. Aboral view of specimen X 130.

FIG. 22. *Apatognathus* sp. nov. A.
a. Inner lateral view of specimen X 43. b. Outer lateral view of specimen X 43.

FIG. 23. *Gnathodus girtyi turritus* Collinson & Druce
a. Lateral view of specimen X 116. b. Aboral view of specimen X 116. c. Oral view of specimen X 116.

FIG. 24. *Geniculatus* sp.
Lateral view of specimen X 327.

FIGS. 25-26. *Magnilaterella robusta* Rexroad & Collinson
25. Inner lateral view of juvenile specimen X 528. 26. Inner lateral view of specimen X 529.

FIG. 27. *Apatognathus porcatus* (Hinde)
Inner lateral view of specimen X 220.



